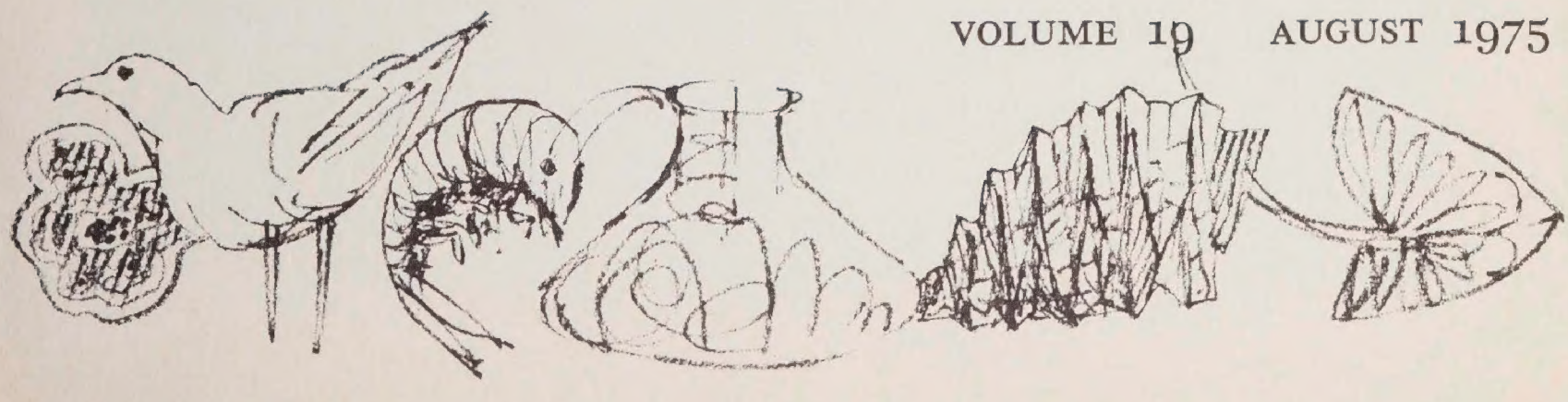
CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 19 AUGUST 1975



CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 19 AUGUST 1975

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Contents

Instructions to Authors iii

Poul E. Heegaard, 1904–1974. *Gordon Gunter* 1

Low-Altitude Aerosol Distribution Along a Barrier Island Coast. *Thomas Whelan III* 3

The Response of Larval Fish, *Leiostomus xanthurus*, to Environmental Stress Following Sublethal Cadmium Exposure. *Douglas P. Middaugh, Wayne R. Davis and Ruth L. Yoakum* 13

Laboratory Observations on Daily Patterns of Burrowing and Locomotor Activity of Pink Shrimp, *Penaeus duorarum*, Brown Shrimp, *Penaeus aztecus*, and White Shrimp, *Penaeus setiferus*. *Donald A. Wickham and Frederick C. Minkler III* 21

Causes and Probable Correctives for Oxygen Depletion Fish Kills in the Dickinson Bayou Estuary: A Field Study and Simplified Algal Assay. *Ken Knudson and Charles E. Belaire* 37

Seasonal Variations in Nearshore Circulation in the Northwestern Gulf of Mexico. *Ned P. Smith* 49

Fiddler Crabs in a Nontidal Environment. *Lawrence W. Powers* 67

Seasonal and Areal Comparisons of Fish Diversity Indices at a Hot-Water Discharge in Galveston Bay, Texas. *Benny J. Gallaway and Kirk Strawn* 79

Summer Growth Depression in the Striped Mullet, *Mugil cephalus L.* *Joseph J. Cech, Jr. and Donald E. Wohlschlag* 91

The Possible Origin of Peculiar *Thalassia testudinum* Reported from Texas as *Posidonia oceanica*. *Calvin McMillan, Yaacov Lipkin and Louis H. Bragg* 101

Day Degree Growth Models for Intertidal Oysters. *Richard F. Dame*..... 107

A Note on Standing Crops of *Spartina alterniflora* in Texas and Florida. *R. E. Turner and J. G. Gosselink* 113

Diel Fluctuations in Catches of Juvenile Brown and White Shrimp in a Texas Estuarine Canal. *Stephen H. Clark and Charles W. Caillouet*..... 119

Plate Correction for Volume 18 (p. 52) from: Key to the Natantia (Crustacea, Decapoda) of the Coastal Waters on the Texas Coast. *Carl E. Wood* 125

POUL E. HEEGAARD
1904–1974

Dr. Poul E. Heegaard was attached to the Zoological Museum at the University of Copenhagen through several research grants over the years. He also taught at the University of Western Australia, the University of Bandung, Java, the American University in Beirut, Lebanon, and worked as visiting zoologist at various marine stations over the world.

Doctor Heegaard obtained the doctor's degree from the University of Copenhagen. He began as an invertebrate morphologist specializing in the crustaceans. He made notable contributions to the morphology and origin of the appendages of crustaceans by doing dissection with a special set of fine tools he devised which permitted work at higher magnifications than anyone had carried out before. Some American zoologists ranked him as the leading crustacean morphologist of his day. He also contributed extensively to the biology of parasitic copepods and the penaeid shrimp.

His connections with the penaeids began in 1948 when he received an invitation from the Texas Game, Fish and Oyster Commission to study the larval history of the commercial shrimp, *Penaeus fluviatilis*. The Rockport location was unsatisfactory for he said the salinity was too low and the temperature was too high and he soon transferred his efforts to the Institute of Marine Science of The University of Texas at Port Aransas, where he was closer to "a very rough and capricious sea" (Heegaard 1953).

His work during that summer resulted in the publication cited, which was freely annotated by me and Martin Burkenroad, and which according to one invertebrate zoologist "finished off poor Heegaard for good". However, this paper still stands as one of the more learned discussions of larval shrimp problems of the family *Penaidae* of the Gulf of Mexico. Who was right about the details is a matter of little importance.

Heegaard later made a monographic contribution to the classification of the pelagic *Penaeidae* of the North Atlantic Ocean, which collections had been made originally by Johannes Schmidt when he was working on the eels, and by a few subsequent workers. These collections were deposited in the Universitetets Zoologiske Museum of Copenhagen.

Heegaard visited Ocean Springs in September 1970 and gave a lecture to the zoological staff of the Laboratory on some problems of crustacean biology and how to solve them through museum collections.

Poul E. Heegaard was not easy to live with or around. He was very sensitive, highly perceptive and quite critical. The intense competition for positions in a small country where, during most of his lifetime, there was only one university and only one Professor of Zoology, did not make for an atmosphere of relaxed friendliness among Danish zoologists. Thus in his native land, Poul E. Heegaard never attained a permanent position but lived and worked under grants, except for periods of teaching in foreign universities. Under these circumstances he

maintained his enthusiasm for zoology to the very end of his life, being in that "a better man than I am Gunga Din"; and it redounds greatly to his credit that under personally difficult conditions he earned for himself a place in the now venerable and respected Danish school of marine zoologists. In this regard he excelled some of his critics who attained stable positions but contributed little. Workers of the future will never hear of them, but Heegaard's name will last a long time, for he was a good zoologist and that really is the basic accolade that a good zoologist seeks.

Doctor Heegaard died of cancer in Copenhagen on February 3, 1974. He was seventy years old. He is survived by his wife and two children by a previous marriage.

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LOW-ALTITUDE AEROSOL DISTRIBUTION ALONG A BARRIER ISLAND COAST

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ABSTRACT

Low-altitude Na aerosol concentration gradients were determined by a method designed to sample airborne particles produced primarily from surf spray along a coast where a diurnal sea breeze system operates. From 1.5 to 2.3 m^3 of air were sampled at 3-hour intervals and analyzed for Na and Mg. Aerosol concentrations were analyzed as a function of wind direction at 1.5 m elevation for a 75-hour time period. The highest concentrations were observed during persistent onshore winds. Periods of offshore and longshore winds generated less aerosol. Average atmospheric Na concentrations at 1.55, 3.1, and 4.6 m above the beach zone were 124.5, 91.3 and 66.3 μg Na/m^3, respectively. Total aerosol concentration was primarily dependent upon wind direction, duration and speed.

INTRODUCTION

Atmospheric sea salts have become an increasingly important area of investigation in recent years. At moderate and high altitudes, seasalt aerosols are an important source of condensation nuclei (Dinger, Howell and Wajciechowski 1970). The quantity and quality of sea-salt particles deposited on land may be important in determining the physical and chemical characteristics of coastal soils and plants (El Swaify, Swindale and Uehara 1968; James 1972). A net positive space charge observed above the surf zone and in the open ocean is due to ejection of droplets of seawater into the atmosphere when bubbles burst at the sea surface (Blanchard 1966).

At least two types of atmospheric sea-salt particles exist which can affect the coastal zone: (1) surf-produced sea spray generated by mechanical dispersion of breaking waves; and (2) aerosol generated in the open ocean by bursting bubbles (Duce and Woodcock 1971; Junge 1972). Airborne sea salts range in size from about 0.5μ (Durbin and White 1961) to 100μ (Junge and Jaenicke 1971). Toba (1965a) concluded that oceanic aerosol concentration generally decreased exponentially with height and that below 1 km the concentration was independent of particle size. Simpson (1972) reported an increase in Na concentration above the trade wind inversion during periods of diurnal change in temperature and humidity. Information is lacking, however, for aerosol generated at the air-sea-land boundary. It is the purpose of this investigation to examine a technique for sampling short-term variation in aerosol concentration at the air-land-sea bound-

ary and to report preliminary results concerning the distribution of low-altitude aerosol along a coast where a diurnal sea-breeze system is in effect.

EXPERIMENTAL PROCEDURE

The field study (Figure 1) was conducted on the Padre Island National Seashore near Corpus Christi, Texas, during September 1972. A 5-km strip of beach was chosen where public use was prohibited. Three air samplers, 1.55 m, 3.1 m and 4.6 m high, were placed approximately 3 m apart on the beach and parallel to the high-tide mark. The air sampler at 1.55 m was maintained throughout the study period. Figure 2 shows the 1.55-m tower, vacuum pump system and glass air sampler.

Air samples containing gases and particles of all sizes were collected by a method similar to that described by Tsunogai, Saito, Yameda and Nakaya (1972). Air was drawn through 250 ml of double-distilled water in Greenburg-Smith glass samplers by vacuum pumps operated from a gasoline generator placed 100 m downwind from the sampling site. Flow rates were calibrated in the laboratory and set with a needle valve at 12 l/min, or 0.75 m^3/hour. Total air volumes of 1.5 to 2.3 m^3 were obtained for individual determinations of Na and Mg by atomic absorption spectrophotometry. The Mg concentration was determined in each sample as an internal check for Na inasmuch as the Mg/Na ratio in worldwide air samples is the least fractionated of the major atmospheric cations with respect to seawater. The average fractionation or E value ($E_{Mg} = [(Mg/Na)_{air}/(Mg—Na)_{seawater}] —1$) for Mg (as indicated in the last column of Table 2) is $+0.065$. Calcium was determined on several representative samples; however,

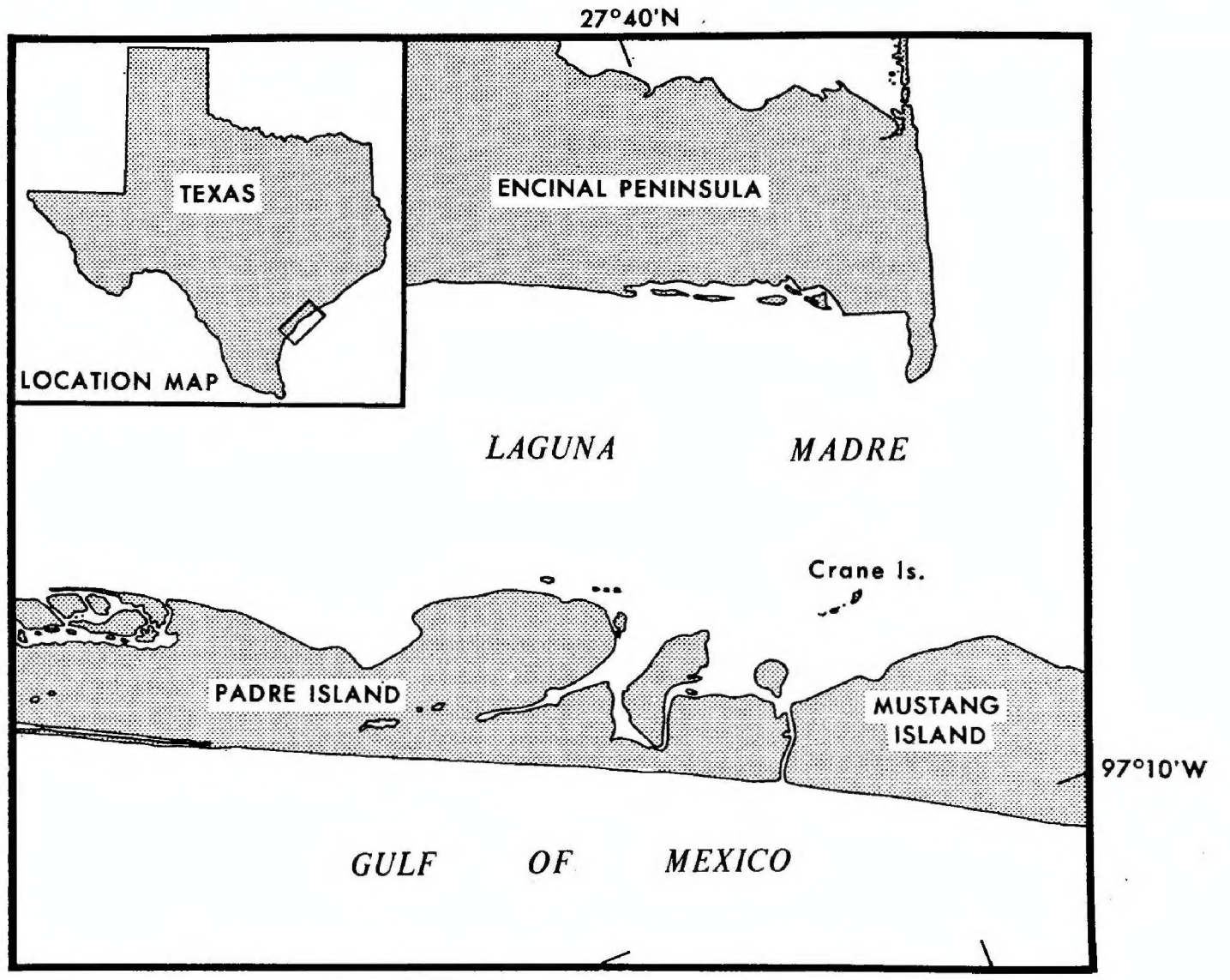

FIG. 1. Location map showing sampling area.

FIG. 2. Photograph of low-altitude aerosol sampling apparatus showing pump, tower, glassware, and wind direction indicator (top).

anomalously high Ca/Na ratios were observed at low wind speeds. This was probably due to contamination by airborne particulate matter of terrestrial origin. Variations in K concentrations were below the analytical certainty of the procedure and are not reported.

Two air samplers set at 1.55 m above the beach were run simultaneously for 6 hours during periods of variable wind speed and direction to measure the overall reliability of the analytical procedure. There was an 8.1% difference between the Na concentrations in the two air samples

taken by this method. The error was probably due to slight differences in the volume of air pumped through the air samplers. A large part of this error could be corrected by using a precise flow control regulator in each system. The fractionation observed for Mg (6.5%) was smaller than the overall error in analytical procedures.

Wind speed and direction at 300 cm above ground level were determined for reference purposes (Climet Instrument Company Model CI-26). Precise measurements of wind speed at the three sampling levels were made according to the method described by Hsu (1971). Supporting wind speed data were obtained from the Corpus Christi National Weather Service.

RESULTS AND DISCUSSION

Aerosol Concentration vs. Wind Direction

Table 1 indicates the Na aerosol concentration at 1.55 m above the high-tide level on the beach; the values are listed according to average wind direction during the sampling period. The wind direction from 0115 on September 13 to 1615 on September 16, 1972, plotted at hourly intervals, is shown in Figure 3. During periods of onshore winds, the average aerosol concentration was 2 to 3 times greater than during offshore or longshore winds. Nine air samples were collected, ranging in Na concentration from 12.0 to 323.6 μg Na/m^3, when onshore winds were recorded. The highest concentration occurred from 0130 to 0430 on September 14, 3 hours after the peak in onshore wind speed during a 48-hour period of continuous onshore winds. The lowest concentration during onshore winds occurred immediately after the directional wind shift from offshore to onshore, from 1230 to 1530 on September 14. Wind speed data were not taken prior to the first air sample collected on September 13; however, data from the Corpus Christi National Weather Service, taken at Corpus Christi, Texas, indicated low onshore wind speeds (95 to 167 cm/sec) from 0000 to 0900 on September 13. This would explain the fairly low aerosol concentration (55.7 μg Na/m^3) observed from 1045 to 1345. Onshore aerosol concentration from 1400 on September 15 to 0030 on September 16 at wind speeds of 448 to 540 cm/sec were lower than at comparable wind speeds the day before. These samples were taken following a directional wind change from offshore (10 hours continuously) to onshore. Thus the data indicate that the duration, as well as wind speed, of onshore winds is important in establishing maximum aerosol concentrations.

Three air samples were collected when the wind direction was offshore (west-northwest). As shown in Table 1, the average aerosol concentration was lower than during onshore winds, ranging from 115.0 to 15.9 μg Na/m^3. The sample from 0515 to 0330 on September 14 (115.0 μg Na/m^3) was taken during a rain shower, which may account for the relatively high concentration resulting from the "washing out" effect of rain observed for atmospheric particles (Engelmann 1968). Low aerosol concentrations observed during offshore winds are reasonable because the source of seawater for aerosol generation is restricted to the Laguna Madre and to Corpus Christi Bay. Low wind speeds were recorded during these periods of offshore winds, a condition which further minimizes the potential for generating aerosols.

A slow shift in wind direction from onshore to longshore was observed on September 16 from 0030 to 1400. The average aerosol concentration during this

TABLE 1

Time, Na concentration (1.55 m), wind speed, and relative humidity for various wind directions

Time (CDT)		Na (μg/m^3)	Wind Speed (cm/sec)
	Onshore Wind		
September 13, 1972			
1045–1345		55.7	331
1415–1715		131.1	445
1800–2100*		129.7	537
2155–0100		213.2	561
September 14, 1972			
0130–0430		323.6	493
1230–1530		12.0	321
September 15, 1972			
1400–1700		39.0	448
1745–2100		61.5	540
2115–0030		31.3	510
	Average	110.8	
	Offshore Wind		
September 14, 1972			
0515–0820*		115.0	227
0845–1145		15.9	234
September 15,1972			
1030–1330		51.1	230
	Average	60.7	
	Longshore Wind		
September 16, 1974			
0030–0330		27.5	230
0400–0700		33.8	510
0730–1030		16.0	382
1105–1400		42.3	450
	Average	29.9	

* Light rain shower.

period was 29.9 μg Na/m^3. At wind speeds comparable to those observed during persistent onshore winds, the average aerosol concentration for longshore winds was about 3 times less. Longshore aerosol concentrations were, however, similar to those observed during short-duration onshore winds on September 15. Again, the data suggest that wind duration, direction (or possibly wind trajectory) and speed are the most important factors controlling low-altitude coastal aerosol concentration.

Vertical Aerosol Gradient

Twenty-four samples were collected from 1045 on September 13 to 1530 on September 14, 1972, during a diurnal sea-breeze cycle. The results in Table 2 show aerosol concentrations at 3-hour intervals for three elevations along the beach. Duce and Woodcock (1971) suggest that aerosols collected below 4 m

FIG. 3. Wind direction at hourly intervals during the sampling period.

probably represent atmospheric sea-salt particles generated predominantly by wave action. The maximum Na concentrations for the 1.55-m, 3.1-m, and 4.6-m towers were 323.6, 190.8, and 147.0 $\mu g/m^3$, respectively.

It should be noted that rain showers were recorded on two occasions, from 1800 to 2100 on September 13 and from 0515 to 0820 on September 14. In both cases the vertical gradient was negligible, and the concentrations were similar, indicating that raindrops scavenged atmospheric particles in a manner similar to that described by Engelmann (1968).

The range of Na concentrations at the three elevations is shown in Figure 4. Duce and Woodcock's (1971) data, reported at 4 m, range from 33 to 100 μg Na/m^3. It is highly unlikely that a significant difference exists between seawater and aerosol Na/Cl ratios below 4 m, thus their total Cl concentrations, taken by

TABLE 2

Temporal variation of wind speed, sodium concentration, and magnesium fractionation

Time (CDT)	Wind Speed (cm/sec)	Concentration Na ($\mu g/m^3$)			^{E}Mg
		1.55 m	3.1 m	4.6 m	
September 13, 1972					
1045–1345	331	55.7	103.4	11.5	+0.31
1415–1715	445	131.1	88.5	30.6	—0.16
1800–2100*	537	129.7	190.8	122.5	—0.08
2155–0100	561	213.2	50.4	147.0	—0.30
September 14, 1972					
0130–0430	493	323.6	109.5	58.8	—0.16
0515–0820†	227	115.0	145.3	112.7	+0.01
0845–1145	237	15.9	27.2	32.7	+0.98
1230–1530	321	12.0	15.3	14.4	—0.08
Average		124.5	91.3	66.3	+0.065

* 45-minute light rain shower.
† Light rain shower.

cascade impactor measurements on the windward coast of Hawaii, were converted to Na concentrations on the basis of the standard seawater ratio of Na/Cl. The range of Na concentration taken by the method reported here is in agreement with atmospheric Na concentrations taken by the cascade impactor technique on a trade wind coast. Total aerosol data reported in previous studies as μg atmospheric sea salts per m^3 of air were converted to μg Na per m^3 of air on the basis of the ratio of Na to total sea salt. Very little variation in Na concentration has been reported above 20 m. The average Na concentration from 1.55 m to 4.6 m, including Duce and Woodcock's (1971) data, generally decreases exponentially with height up to 4.6 m. This observation is in agreement with Toba's (1965b) assumption concerning the aerosol concentration gradient from the sea surface to 10 m above the open ocean.

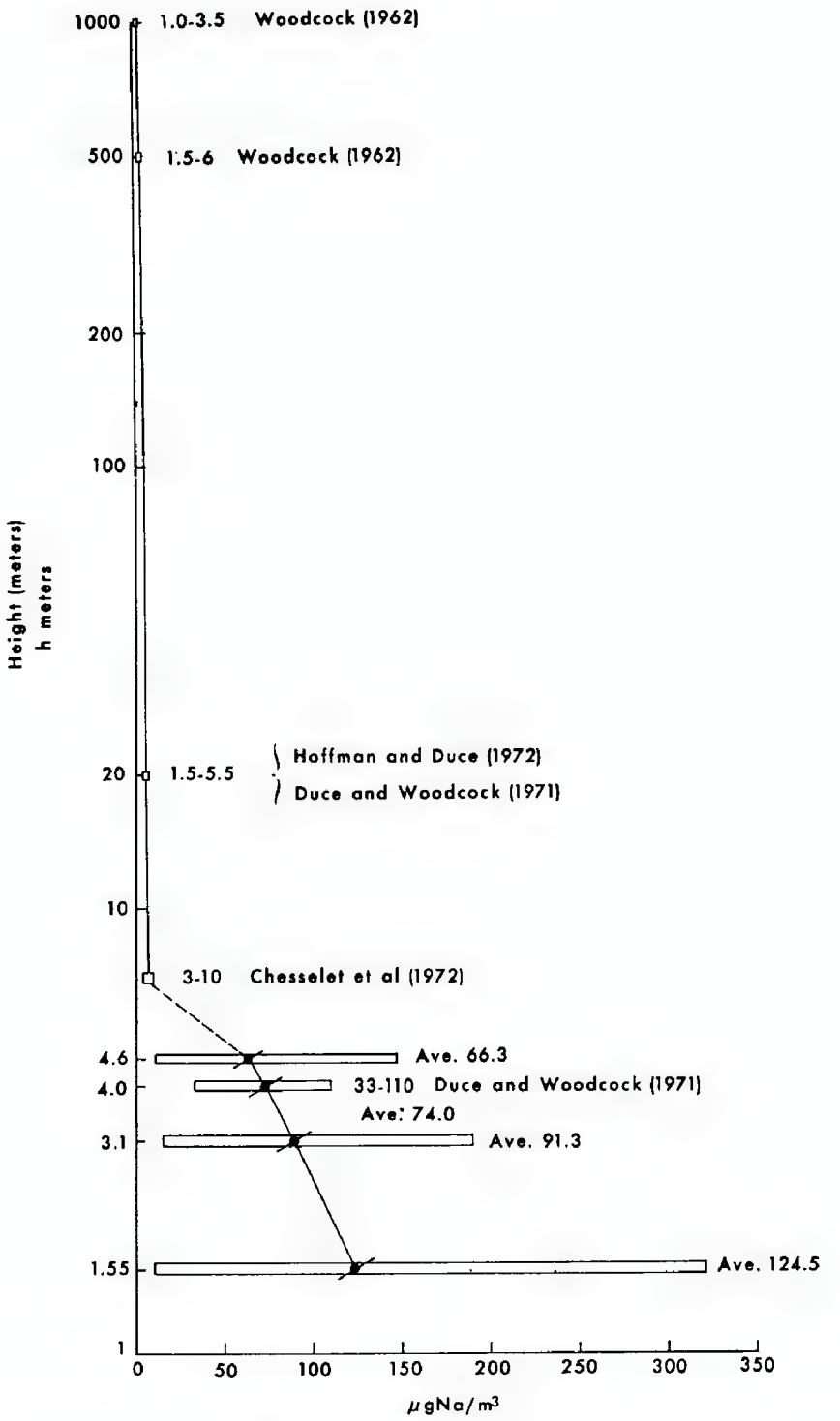

FIG. 4. Log plot of the vertical sodium concentrations in aerosol from 1.55 m to 1,000 m.

CONCLUDING REMARKS

This preliminary case study of aerosol distribution along a barrier island coast indicated that low-altitude aerosol concentration appears to be primarily regulated by wind direction, duration and speed. During persistent onshore winds (24 hours or greater), aerosol concentration increased with increasing wind speed. During offshore and longshore wind directions of short duration, no correlation with wind speed was observed.

Total aerosol concentrations at three elevations (reported as Na concentration) were consistent with previous studies. Average aerosol decreased exponentially with height from 1.55 to 4.6 m above sea level.

Additional experiments which include longer term sampling over a greater variety of wind, wave and climatic conditions and additional supporting meteorological data, such as relative humidity and wind trajectory, are necessary to extend the results of this investigation.

ACKNOWLEDGMENTS

I wish to thank Dr. S. A. Hsu of the Coastal Studies Institute for helpful comments and critical review of this manuscript. This study was sponsored by the Geography Programs, Office of Naval Research, under Contract N00014–69–A-0211–0003, Project NR 388 002, with the Coastal Studies Institute, Louisiana State University. Appreciation is extended to the National Park Service, Padre Island National Sea Shore, for logistic help and to the Corpus Christi National Weather Service for supplying supporting meteorological data.

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THE RESPONSE OF LARVAL FISH, *LEIOSTOMUS XANTHURUS*, TO ENVIRONMENTAL STRESS FOLLOWING SUBLETHAL CADMIUM EXPOSURE[1]

Douglas P. Middaugh, Wayne R. Davis and Ruth L. Yoakum[2]

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ABSTRACT

The toxicity of cadmium to larval fish, *Leiostomus xanthurus*, was studied. An incipient LC_{50} concentration of approximately 0.2–0.3 mg/1 cadmium was first estimated. Subsequent short-term sublethal tests were conducted to determine the relationship of cadmium exposure and accumulated whole body residues of the metal on the response of larvae to thermal stress and low dissolved oxygen. Results of this study indicated a significant decrease (α=0.05, t-Test) in the critical thermal maximum (CTM) for larvae exposed to 0.5 and 0.8 mg/1 cadmium for 96 hours at 20C. Significant decreases (α=0.05, χ^2) in survival of larvae subjected to a dissolved oxygen (DO) level of 1.6 mg/1 after exposure to 0.5 and 0.8 mg/1 cadmium were also observed.

INTRODUCTION

Recent studies have demonstrated both lethal and sublethal effects of cadmium on various estuarine organisms (Gardner and Yevich 1970; Jackim, Hamlin and Sonis 1970; Eisler 1971; O'Hara 1972). Although these studies have shown the deleterious effects of cadmium under various environmental conditions, they did not attempt to assess the response of organisms pre-exposed to sublethal concentrations of cadmium and then subjected to environmental stress.

The present study was initiated to determine both lethal and short-term sublethal responses of larval spot, *Leiostomus xanthurus*, to cadmium. An incipient LC_{50} curve (Sprague 1964; 1970) was used to estimate the lethal effect of cadmium on larvae in flowing seawater. Bioassays were then conducted at sublethal concentrations of cadmium and larvae subjected to thermal stress or low dissolved oxygen levels to determine the effect of pre-exposure to cadmium on survival.

MATERIALS AND METHODS

Larval spot (total length 10–15 mm, mean wet weight 0.1 g) were collected during March and April, 1973 from We Creek, a tidal tributary of the North Edisto River estuary, Wadmalaw

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[2] Present address: U. S. Environmental Protection Agency, Gulf Breeze Environmental Research Laboratory, Bears Bluff Field Station, Box 368, John's Island, S.C. 29455.

Island, S.C. Collections were made on incoming tides during moonless or overcast nights with a 0.5 mm mesh, 1 m surface plankton net. Ambient seawater temperatures ranged from 14.5 to 21.3 C and salinity from 14 to 23 parts per thousand (ppt).

Larvae were transferred to the laboratory and stocked in rectangular flow-through tanks, 60 cm × 50 cm × 25 cm (volume 80 l) with a flow rate of 40 l of unfiltered seawater per hour. Fish were fed recently hatched *Artemia nauplii* twice daily and maintained in the laboratory for a minimum of 5 days prior to use in bioassays.

Incipient LC_{50}

To determine the incipient LC_{50}, 20 larvae were placed in each of 8 plexiglas[1] flow through aquaria, 27.5 cm × 15 cm × 8.7 cm (volume 4 l), with a flow rate of 18 l of seawater per hour. After 5 days of acclimation of larvae to the new aquaria, cadmium was introduced by syringe pump at nominal concentrations that ranged from 10 to 0.1 mg/l (Table 1). During the 5-day acclimation and subsequent 200-hour exposure to cadmium, larvae were fed *Artemia* nauplii twice daily. Water temperature ranged from 15 to 22 C and salinity from 16 to 19 ppt during this bioassay.

Checks for death were made at maximum intervals of 8 hours and the time to 50 percent mortality was recorded for each exposure concentration of cadmium. Survivors were removed from their respective treatment aquaria, rinsed in deionized water, and frozen for subsequent residue analysis by atomic absorption spectrophotometry (Eisler 1971).

Short-term Sublethal Exposure to Cadmium

After constructing an incipient LC_{50} curve, a series of bioassays was conducted at 3 sublethal concentrations of cadmium based on the estimated incipient LC_{50}. Nominal concentrations of 1.0, 0.5 and 0.1 mg/l were used. These bioassays were conducted in plexiglas aquaria measuring 55 cm × 25 cm × 17.5 cm (volume 18 l) and receiving 18 l of seawater per hour. They were designed for short-term exposure of larvae to sublethal cadmium concentrations. Prior to exposure, 120 larvae were placed in each aquarium and accliminated for 5 days. Larvae were fed *Artemia* nauplii twice daily during acclimation and during the 96-hour exposure interval. Water temperature was maintained at 20 ± 1 C with an immersion heater; the salinity ranged from 17 to 20 ppt.

After exposure to cadmium for 96 hours, replicate samples of 4 to 6 fish were removed from their respective aquaria for residue analysis. The remaining larvae were subjected to thermal stress or to low dissolved oxygen (DO) levels.

To determine if pre-exposure to sublethal levels of cadmium would result in a shift in the

TABLE 1

Nominal and measured concentrations of cadmium in unfiltered seawater used to determine the incipient LC_{50} for larval spot

Nominal Conc. mg/l	Measured conc. mg/l
10.0	8.0
5.0	6.0
3.0	2.4
1.0	0.8
0.5	0.6
0.3	0.3
0.1	0.1

[1] Mention of commercial products does not constitute endorsement by the Environmental Protection Agency.

Critical Thermal Maximum (CTM) (Hutchinson 1961; Bridges 1971), larvae (2 groups of 5) were transferred from their respective exposure aquaria to a 20 l water bath at 20 ± 1 C and ambient salinity. The bath was heated at a rate of approximately 1.0 C/5 minutes with a rheostat-controlled immersion heater. The temperature at which each fish elicited a death response (flaring of the operculars was the index for this response) was measured to the nearest 0.1 C and recorded. The mean, standard deviation, standard error and range for each assay was obtained and plotted, using techniques outlined by Hubbs and Hubbs (1946).

To determine the response of fish to low environmental oxygen levels following exposure to cadmium, 4 to 8 replicate groups of 6 larvae from each concentration of cadmium were placed in 500 ml Erlenmeyer flasks at 20 ± 1 C and ambient salinity. Replicate flasks were then attached to a flowing seawater system with DO concentrations of 1.6, 3.5 and 6.5 mg/l at 20 ± 1 C. This system utilized nitrogen sparged seawater and is similar to one described in detail by Morrison (1971). A flow rate of 20 ml/minute through each flask was maintained to insure constant DO levels which were monitored at 3-hour intervals with a YSI Model 51-A Oxygen Meter. Percentage survival at each dissolved oxygen level and cadmium exposure concentration was recorded at the end of 24 hours.

Residue Analysis

Whole body burdens of cadmium (μg Cd/g ash) present in larvae from the incipient LC_{50} bioassay and subsequent short-term sublethal exposure bioassays were determined by atomic absorption spectrophotometry. Groups of 4 to 6 fish, total wet weight approximately 0.5 g, were placed in tared crucibles and dried for 4 hours at 90 C. Dried larvae were ashed at 425 C for 24 hours. Crucibles were cooled to ambient temperature in a desiccator and reweighed. One ml of concentrated HNO_3 was added to each crucible. After 1 hour, the digested ash was pipetted into a 10 ml volumetric flask. Each crucible was rinsed twice with 2 ml aliquots of deionized water and each sample was aspirated directly into a Perkin-Elmer Model 403 atomic absorption spectrophotometer. Recovery rates for spiked samples indicated less than 3 per cent loss of cadmium during the drying, ashing and digestion process. Replicate water samples taken at 48-hour intervals from the incipient LC_{50} and sublethal exposure bioassays were aspirated directly into the spectrophotometer.

RESULTS AND DISCUSSION

The incipient LC_{50} curve for larval spot exposed to cadmium (Figure 1) is similar to those constructed by Powers (1917), Carpenter (1927) and Sprague (1964) to demonstrate the lethal action of other metallic salts for fish. An incipient LC_{50} of 0.2-0.3 mg cadmium per liter was estimated by determining the portion of the time-survival curve which is asymptotic to the time axis and reading the exposure concentration from the abcissa below (Sprague 1964).

Larval spot exposed to the four highest concentrations of cadmium, 0.8-8.0 mg/l, died rapidly with no indication of irritability prior to death. Larvae subjected to concentrations of 0.3 and 0.6 mg/l exhibited a phase of disoriented swimming at the surface of treatment aquaria for 5–7 hours before dying.

Surviving larvae from the highest exposure concentrations, 0.8–8.0 mg/l cadmium, accumulated whole body burdens (μg Cd/g ash) at least 300 percent greater than those exposed to concentrations ranging from 0.1–0.6 mg/l (Table 2). Whole body burdens of cadmium measured in survivors and behavioral responses of larvae that succumbed at the 0.3 and 0.6 mg/l exposure concentrations suggest a change in rate of accumulation and toxic effect of the metal at concentrations near the estimated incipient LC_{50} of 0.2–0.3 mg/l. No larvae died at an exposure concentration of 0.1 mg/l cadmium after 200 hours of exposure. Toxic

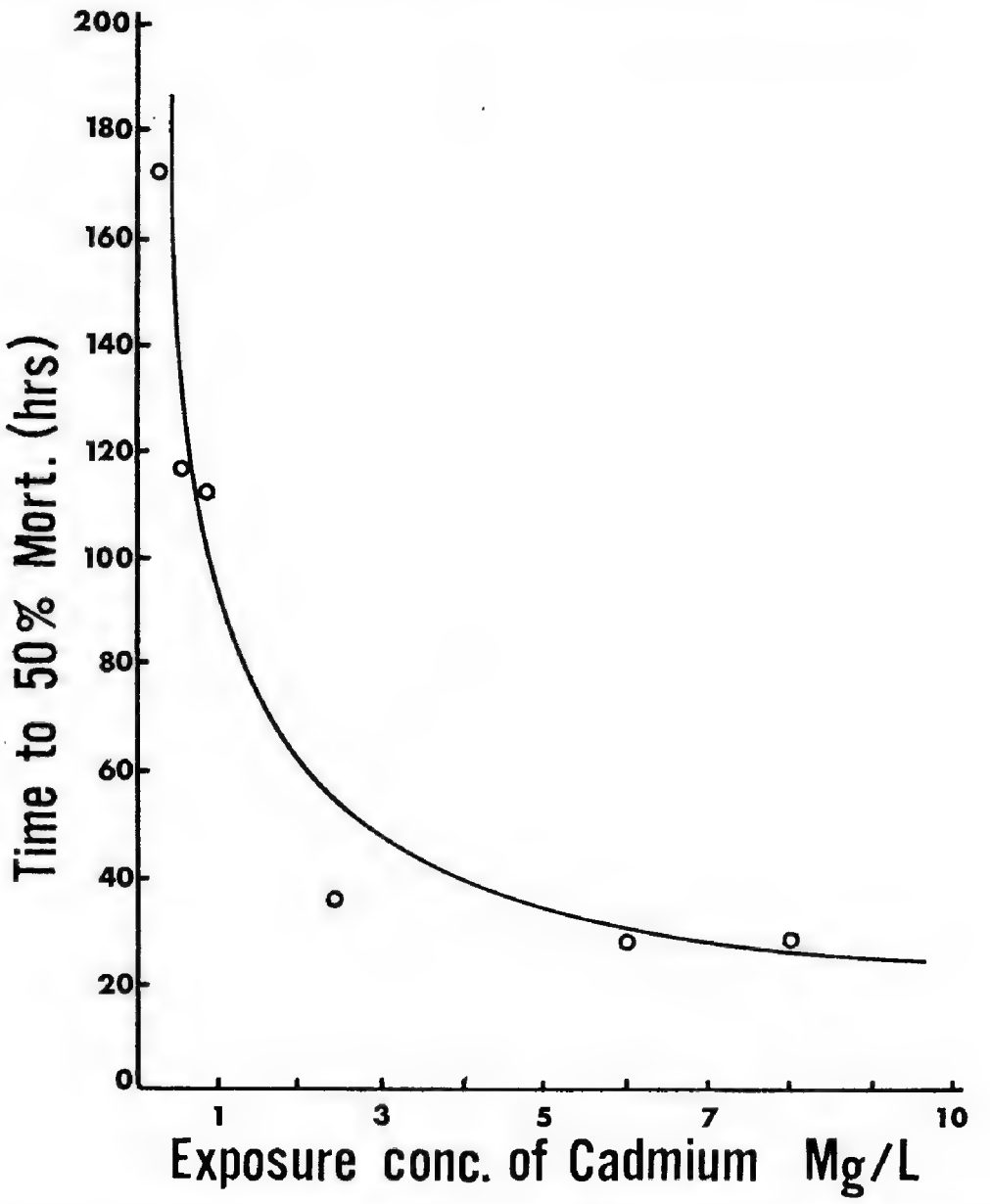

FIG. 1. Toxicity curve for larval spot exposed to cadmium in flowing seawater. The incipient LC_{50} is approximately 0.2–0.3 mg/l cadmium.

body burdens may have occurred at this exposure concentration if the test had been prolonged (Table 2).

In subsequent short-term sublethal exposures, concentrations of cadmium measured in respective treatment aquaria were 0.09, 0.5 and 0.8 mg/l. At the 0.8 mg/l concentration, 20 percent of the larvae died by the end of the 96-hour exposure interval. No deaths occurred at exposure concentrations of 0.09 and 0.5 mg/l cadmium. Whole body burdens (μg Cd/g ash) measured for replicate samples taken from each treatment aquarium immediately prior to conducting thermal resistance or DO stress tests were 0.09 mg/l (18,23); 0.5 mg/l (42,43); and 0.8 mg/1 (112,162) respectively.

The CTM of larvae exposed to concentrations of 0.5 and 0.8 mg/l cadmium for 96 hours was significantly less (α=0.05, t-Test) than that of controls. A slight decrease in the thermal resistance of larvae exposed to 0.09 mg/l cadmium was also observed but was not significant (Figure 2). Since our heating rate, 1.0 C/5 minutes, was slower than the rate of 1.0 C/minute used by Bridges (1971) and Hoss, Coston and Hettler (1971) it is possible that some temperature acclimation occurred during the CTM tests with respective groups of spot larvae.

TABLE 2

Body burdens of cadmium detected in replicate whole fish samples from survivors of the incipient LC_{50} bioassay. Pooled groups of 4–6 larvae were used for each replicate determination

Measured exposure concentrations mg/l	Time to 50 % mort. (hrs)	Replicated Cd body burdens (μg Cd/g ash) A	B
8.0	30	211	269
6.0	30	248	346
2.4	36	170	243
0.8	112	120	190
0.6	116	43	56
0.3	172	40	43
0.1	[1]	27	29

[1] No deaths at the end of 200 hours of exposure.

Survival data for each concentration of cadmium and DO regime indicated a decline in resistance to oxygen stress for larvae exposed to cadmium (Table 3). The number of survivors decreased with increased cadmium exposure concentrations and body burdens, especially at the two lowest DO levels. Chi-square analysis with Yates correction (Snedecor 1956) of the response of individuals from each exposure concentration of cadmium at the three DO levels indicated that there was no significant difference (α=0.05) in survival for control and treated larvae maintained at 6.5 or 3.5 mg/l oxygen. The lowest oxygen concentration tested, 1.6 mg/l resulted in a significant decrease in the survival of larvae pre-exposed to 0.5 and 0.8 mg/l cadmium compared to the number of controls surviving at this DO level.

Skidmore (1964) reviewed the effects of water hardness, DO and water temperature on the survival time of fish exposed to zinc in freshwater. In general, the survival time of fish decreased with increased temperature and decreased oxygen concentrations. Amend, Yasutake and Morgan (1969) attributed increased mortality in rainbow trout, *Salmo gairdnerii*, exposed to mercury under elevated temperature and suppressed DO levels to increased metabolic activity. Hoss *et al.* (1971) found that simulated temperature increases encountered by entrained post-larval and juvenile estuarine fishes resulted in increased oxygen consumption and death if the thermal gradient was severe. Larval spot, menhaden and pinfish acclimated to 15C had respective CTM of 31.1, 29.4 and 31.0C at a heating rate of approximately 1C/minute.

Exposure of larval spot to elevated temperature regimes or suppressed DO levels in this study was performed to determine the effect of short-term sublethal metal toxicity on their response to these stress factors. At the two highest exposure concentrations of cadmium, 0.5 and 0.8 mg/l, significant decreases in the CTM occurred. Significant reductions in the resistance of cadmium exposed larvae to a suppressed DO level of 1.6 mg/l were also observed.

Rapid accumulation of cadmium by larval spot in the incipient LC_{50} bioassay and subsequent short-term sublethal exposures indicate that the metal is readily

TABLE 3

Number of survivors/non-survivors of cadmium exposed larval spot subjected to three dissolved oxygen levels for 24 hours

Measured concentration cadmium mg/l	Number of survivors/non-survivors DO conc. mg/l 1.6	3.5	6.5
Control	15/21	34/2	36/0
0.09	6/18	22/2	24/0
0.5	2/22	15/9	34/2
0.8	0/24	9/27	40/8

absorbed by this species. Significant reduction in the capability of larvae to survive thermal stress or low dissolved oxygen after exposure to sublethal concentrations of cadmium demonstrates the potential detrimental effect of this metal in the marine environment.

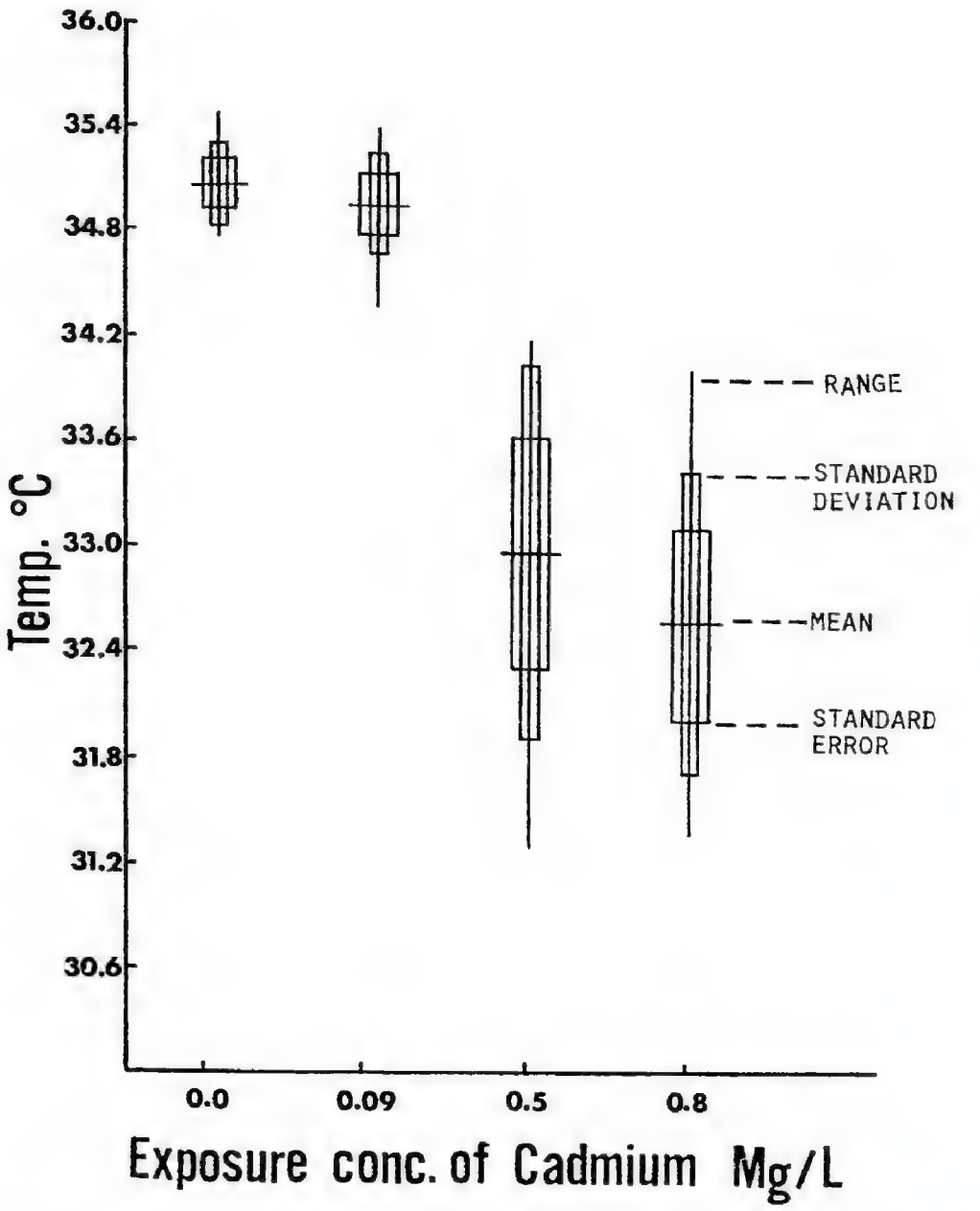

Fig. 2. Critical thermal maximum determinations for larval spot pre-exposed to short-term (96-hr) sublethal concentrations of cadmium.

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LABORATORY OBSERVATIONS ON DAILY PATTERNS OF BURROWING AND LOCOMOTOR ACTIVITY OF PINK SHRIMP, *PENAEUS DUORARUM*, BROWN SHRIMP, *PENAEUS AZTECUS*, AND WHITE SHRIMP, *PENAEUS SETIFERUS*[1]

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ABSTRACT

The daily patterns of burrowing and locomotor activity of *Penaeus duorarum*, *P. aztecus*, and *P. setiferus* were observed in the laboratory under artificial light regimes in synchrony with the environment, advanced in phase by six hours relative to environmental daylight, and with constant light. Observations were also made during light regimes having a nocturnal low-light intensity that required the use of an image-intensifier TV-camera system.

The activity of *P. duorarum* was nocturnal; all individuals were inactive or burrowed during the day. *P. aztecus* activity was also nocturnal; however, individuals had a greater diurnal tendency to remain quiescent on the substrate and not burrow. *P. setiferus* was usually more active than the other two species, with most activity occurring nocturnally. Burrowing was not observed in *P. setiferus*, although individuals were quiescent on the substrate or in shallow depressions for periods up to several hours during the day. The responses of each species to changes in, and level of, light intensity and the rhythmic persistence of their activity pattern appeared to decrease in order for *P. duorarum*, *P. aztecus*, and *P. setiferus*.

INTRODUCTION

Diurnal patterns of burrowing and locomotor activity have been reported for various species of penaeid shrimp (Dakin 1938; Williams 1955, 1958; Racek 1957, 1959; Dall 1958; Menon & Raman 1961; Fuss 1964; Fuss & Ogren 1966; Kutty & Murugapoopathy 1968). Racek (1959) reported daily periods of emergence for three penaeid species, held in constant laboratory conditions, differed among the species observed but were nearly constant for each species. The activity of pink shrimp, *Penaeus duorarum*, under experimental conditions shows a rhythmic component, the expression of which may be subject to modification by light

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and various other environmental factors (Fuss & Ogren 1966; Wickham 1967; Hughes 1968). Differences in the periodicity of locomotor activity or burrowing among the principal commercial shrimp species in the Gulf of Mexico (i.e., pink shrimp, *P. duorarum*, brown shrimp, *P. aztecus*; white shrimp, *P. setiferus*) have been indicated from commercial trawl catches.[3] The behavior of these penaeids, however, has not previously been subjected to simultaneous, comparative experimental study.

We observed the periods of burrowing and locomotor activity for pink, brown, and white shrimp captured at the same time from the same area and held in separate aquaria while the light intensity and the light/dark cycle were altered. Our purpose was to identify behavioral differences in burrowing and locomotor activity, the presence and relative persistence of behavioral patterns and whether behavioral alterations would result from changes in pattern and strength of cyclic stimuli. Differences in patterns and persistence of activity and the significance of light stimuli in modifying behavior would affect experimental design development for penaeid shrimp studies, suggest reasons for observed changes in the availability of shrimp to capture with various gear, and indicate directions for future research to identify causes for and mechanisms of controlling shrimp behavior.

MATERIALS AND METHODS

Juvenile and sub-adult penaeids were collected in November 1971 from the Mississippi Sound off Pascagoula, Miss. We started collecting live shrimp with a 5.4-m (18-ft) shrimp trawl at 1800 hr the evening preceding experiment initiation. The catch was immediately sorted at the completion of each 10-min drag. Healthy-appearing shrimp were separated by species and placed in covered containers of aerated water for transportation to the laboratory. At the laboratory, species identifications were confirmed and 10 individuals of each species were placed in separate aquaria by 0100 hr the morning a set of experimental observations were initiated. Fresh shrimp were captured for each set of experiments. Sex and total length were determined for all experimental animals at the termination of each experiment and a summary of these data are presented in Table 1.

The study area containing six 95-liter (25 gal) aquaria was enclosed by a light-proof curtain. Experimental and contro lareas, both containing three aquaria—one each of pink, brown, and white shrimp—were isolated within separate light-proof chambers (Fig. 1). Each aquarium contained a shell/sand substrate 6–8 cm deep and water at 22 C and 27‰ salinity which was constantly aerated and circulated through outside filters. Water in the Mississippi Sound ranged from 18–20 C and 29–31‰ on the nights shrimp were captured.

Light sources were 30-w incandescent lamps mounted above the aquaria in each chamber and light intensities were regulated with variable transformers. An automatic timer switch (Wickham, Cagle and Hightower 1971) controlled the light-dark cycle and provided a gradual transition between light regimes. A white cloth screen above each aquaria diffused the light and inhibited shrimp from jumping out of the aquaria. Shrimp were maintained under an artificial light-dark cycle (L/D 11:13) unless this light regime was modified for specific experiments. The control bright/dim transition occurred between 1700 and 1800 hr and the dim/bright transition between 0600 and 0700 hr. This provided a cyclic light regime which coincided with environmental day and night.

[3] According to *Ferez-fartane* (1969), pink and brown shrimp from the northern Gulf of Mexico are restricted to the subspecies *P. duorarum duorarum* and *P. aztecus aztecus*, respectively.

TABLE 1

Sex and total body length of shrimp by species for each behavioral observation

Experiment	Type of Aquarium	Pink shrimp, *P. duorarum*			Brown shrimp, *P. aztecus*			White shrimp, *P. setiferus*		
		TOTAL LENGTH		SEX	TOTAL LENGTH		SEX	TOTAL LENGTH		SEX
		Range(mm)	$\bar{x}$	M/F	Range(mm)	$\bar{x}$	M/F	Range(mm)	$\bar{x}$	M/F
Control intensity light regime	Control	82–110	101	6/4	93–123	103	3/7	109–159	135	6/4
	Experimental	83–107	93	2/8	75–115	106	6/4	106–161	131	4/6
Constant light and 6-hour light regime phase advance	Control	80–111	98	7/3	81–106	94	4/6	87–108	99	5/4
	Experimental	74–110	93	6/4	86–110	96	4/6	90–108	97	4/5
Low-intensity light regime	Control	91–116	105	4/6	94–113	104	5/4	92–118	106	6/3
	Experimental	82–115	103	5/5	95–111	102	5/5	85–116	100	6/4

Photometric light measurements were made using a Gamma Scientific, Inc., Model 2020 photometer[4] with a photopic filter to adjust the photomultiplier to the standard luminosity curve. The photometer was coupled to a fiber optic probe with a 180° cosine head sealed for use under water. Light intensity measurements were made with the probe inside each aquarium and the sensor head at the level of the substrate surface directed upward. Light intensity on each aquarium substrate surface was 3×10^{-1} lux during bright periods and 3×10^{-3} lux during dim periods, unless altered for specific experiments. The criteria for establishing the dim-light intensity was the minimum light at which visual observations could be accurately obtained. The bright-light intensity was limited by lamp size and adjusted to provide a two order of magnitude increase above the dim-light intensity.

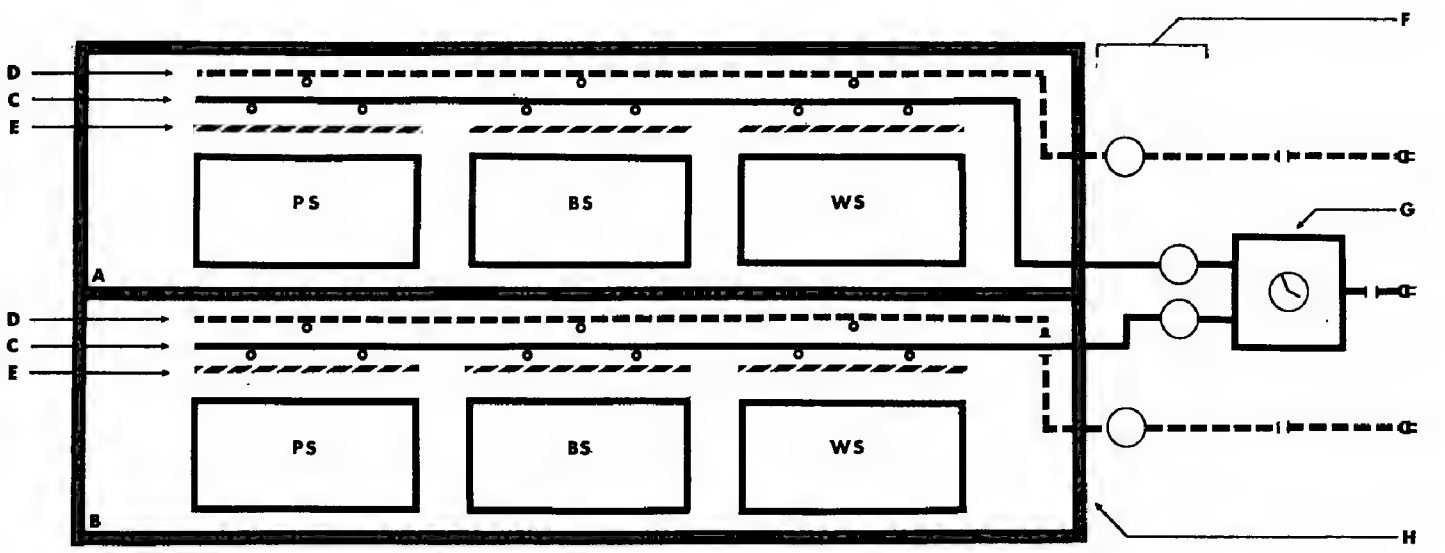

FIG. 1. Schematic illustration of the aquaria arrangement during the shrimp behavior observations. (A) Control group aquaria; (B) Experimental group aquaria; (C) 30-watt bright incandescent lamps; (D) Lamp system for constant dim light; (E) Light diffusing screens; (F) Variable power transformers; (G) Automatic timer switch; (H) Light-proof enclosure; (PS) Pink shrimp; (BS) Brown shrimp; (WS) White shrimp.

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

An RCA low-light-level image intensifier TV-camera system[5] with a 55 mm f 1.4 lens was used during experimental observations with a relatively low-intensity-light cycle (Figs. 2 and 3) when experimental bright- and dim-light intensities were reduced to 3×10^{-3} lux and less than 1×10^{-4} lux (i.e., below the accurate sensitivity limits of the photometer but approximately 3×10^{-5} lux), respectively. This low-intensity experimental-light regime had an approximate two orders of magnitude bright-dim-period intensity differential as did the 3×10^{-1} lux bright and 3×10^{-3} lux dim-light periods used for the control aquaria light regime.

Visual observations of shrimp behavior in each aquarium were made at least once every 30 min. During the hour preceding and following light intensity changes in either the experimental or control environment, observations were increased to once every 15 min. Numerical counts of individual shrimp exposed, walking, and swimming, as well as descriptive behavioral data, i.e., burrowing methods, were recorded during these observations. Exposed shrimp were defined as those more than half exposed and included individuals resting on the substrate, walking, or swimming. The number of shrimp that swam off the bottom during a randomly selected 1-min interval was used as a rough index of swimming activity. To eliminate activity patterns induced by feeding, the shrimp were not fed during these experiments (Hughes 1968).

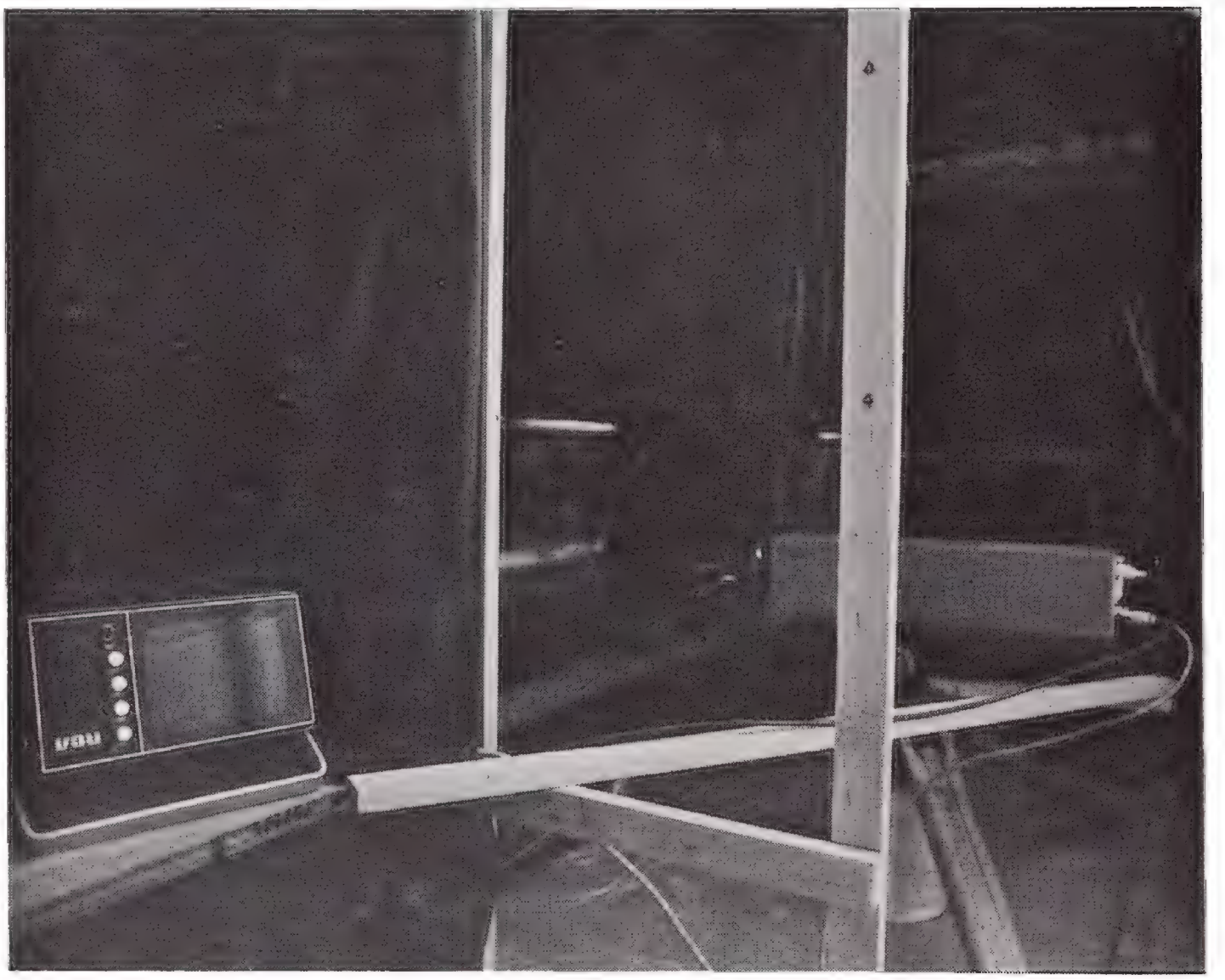

FIG. 2. The low-light-level image intensifier TV system and experimental aquaria arrangement used during low-light-level shrimp behavior observations. The light-proof curtain separating the monitor and image intensifier has been removed for this photograph.

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[5] On loan from NMFS, Southeast Fisheries Center, Fisheries Engineering Laboratory, Mississippi Test Facility, Bay St. Louis, Miss.

FIG. 3. Photograph of experimental shrimp in light of 3×10^{-5} lux taken from the monitor screen of the low-light-level image intensifier TV system.

RESULTS

Activity Patterns Under Control Conditions

We established pink, brown, and white shrimp in the experimental aquaria subject to conditions identical to those in our control aquaria providing a concurrent replication to determine the pattern of, and variability in, burrowing and locomotor activity that could be expected from each species. Each species exhibited differences in the amount and pattern of this type of daily activity (Figs. 4 and 5).

Pink shrimp activity was nocturnal with almost all individuals inactive or burrowed during the bright-light regime occurring during the environmental daylight hours. These shrimp emerged from their burrows during the 1-hr bright/dim transition; at least 80 percent had normally emerged by the end of this transition. A peak of activity (i.e., illustrated by the percent swimming index, Fig. 5) frequently occurred immediately following the onset of the dim-light regime. Activity fluctuated between quiescent periods with little movement and active periods with most of the shrimp swimming and walking. The number of shrimp exposed often decreased during the waning hours of the dim-light regime. A peak of locomotor activity was occasionally observed just prior to the dim/

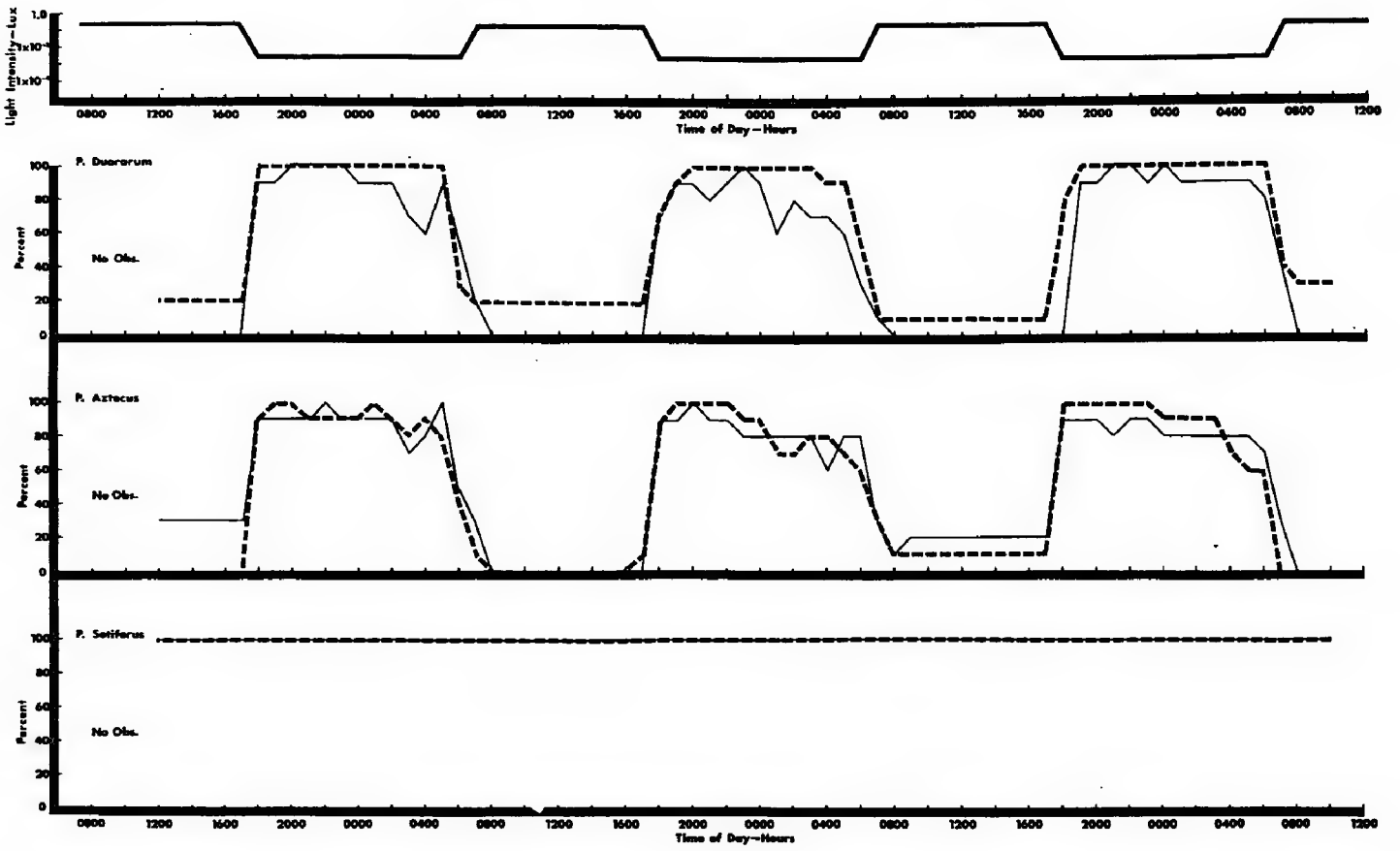

FIG. 4. Pattern of burrowing and emergence shown by percent of *P. duorarum*, *P. aztecus*, and *P. setiferus* exposed under identical control light conditions of L/D 11:13 and 3×10^{-1} and 3×10^{-3} lux, respectively, in synchrony with environmental day/night in both control and experimental aquaria. Shrimp behavior in control aquaria illustrated with solid line and with dashed line in the experimental aquaria.

bright transition. Shrimp not burrowed at the onset of the 1-hr dim/bright transition often burrowed during this period. Pink shrimp usually all burrowed or became immobile on the substratum within the first hour of the bright-light regime. The burrowing behavior of *P. duorarum* was described in detail by Fuss (1964).

Brown shrimp were primarily noctural and had an activity pattern similar to that of pink shrimp. All brown shrimp were active at some time during the dim-light regime and most tended to burrow during the bright regime. Individual brown shrimp would occasionally emerge during the bright-light regime for varying periods and then burrow again so that a few individuals might be seen on the surface throughout the day. Emergence and associated locomotor activities began during the bright/dim transition with most shrimp becoming active by the onset of the dim-light regime. The number of brown shrimp exposed often decreased during the waning hours of the dim regime. The behavior and methods involved in brown shrimp burrowing appeared to be similar to the methods described for pink shrimp.

White shrimp were more active than pink or brown shrimp. They were exposed on the substrate surface or swimming off the bottom day and night and never burrowed during our observations. Swimming activity began during the bright-dim transition and peaks of swimming activity occurred throughout the nocturnal dim-light regime on the first day of each observation series. Swimming

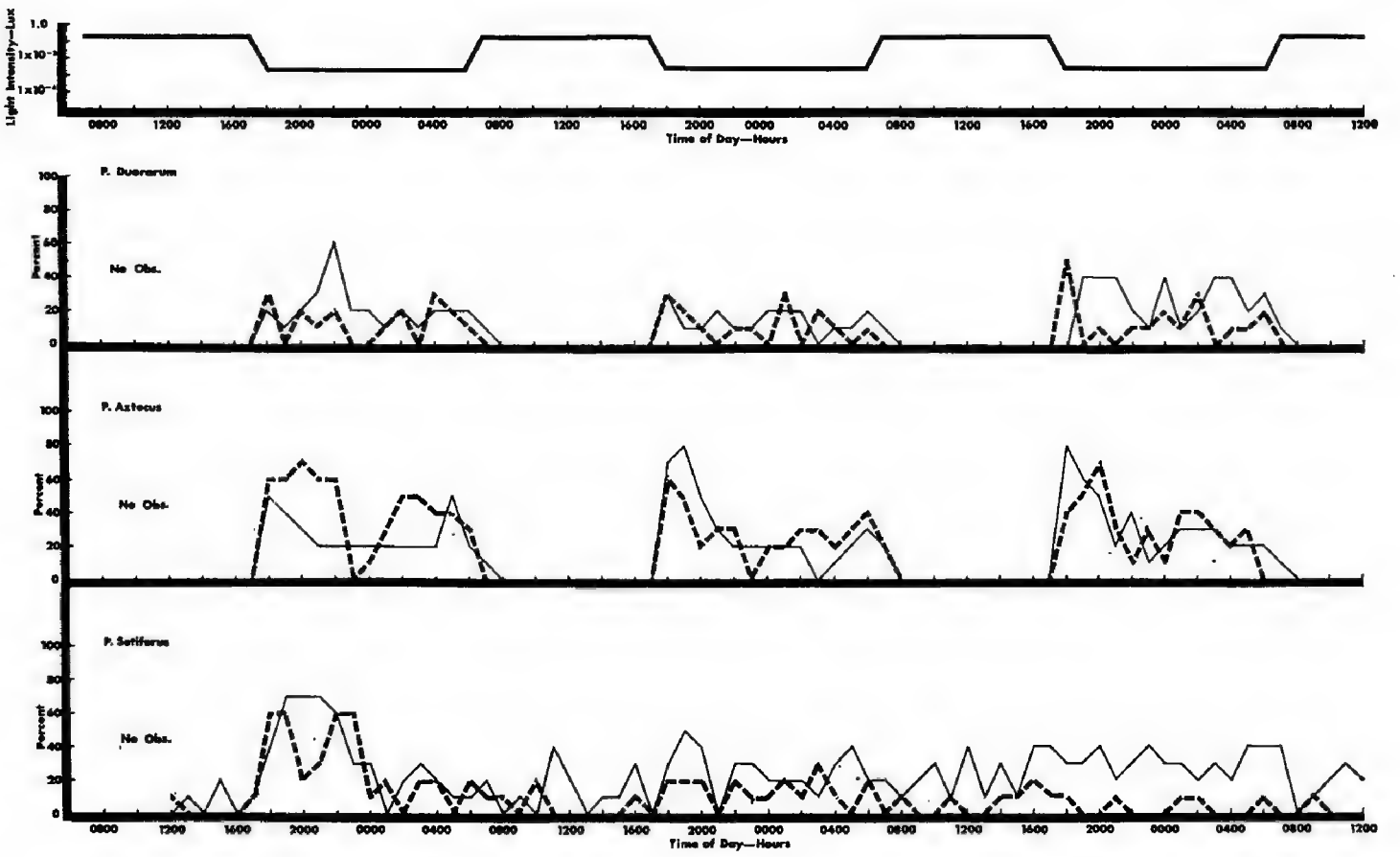

FIG. 5. Pattern of swimming activity associated with the shrimp in Figure 4 shown by the percent of *P. duorarum*, *P. aztecus*, and *P. setiferus* swimming during a 1-min interval for each observation period. The shrimp were held under control light conditions of L/D 11:13 and 3×10^{-1} and 3×10^{-3} lux, respectively, in synchrony with environmental day/night in both control and experimental aquaria. The percent of shrimp swimming in control aquaria illustrated with a solid line and with dashed line in the experimental aquaria.

and walking activity became less frequent during the initial bright regime. During succeeding light cycles activity peaks increasingly occurred irrespective of the light regime. Often 50 percent or more of the white shrimp were quiescent for periods up to several hours during the bright regime of the initial observation cycle. During quiescent periods white shrimp either remained motionless on the substrate or settled into a depression scoured in the substrate by rapidly fanning their swimmerets (pleopods). This depression-forming behavior was identical to the initial phase of one type of burrowing behavior reported for pink shrimp by Fuss (1964).

Effects of Light Intensity on Activity

We compared the activity patterns of shrimp receiving control aquaria light intensities with those subjected experimentally to a relatively low intensity light cycle. This was done to determine whether the control dim-light regime, the minimum intensity required for observations with the unaided dark-adapted human eye, would suppress or change the activity pattern characteristics observed under lower intensity light conditions. The activity pattern for each species under control and experimental low intensity cyclic light conditions 3×10^{-1} to 3×10^{-3} and 3×10^{-3} to 3×10^{-5}, respectively, is shown in Figure 6.

We observed little difference in the general activity patterns from that previously described. The number of shrimp exposed and times of emergence and

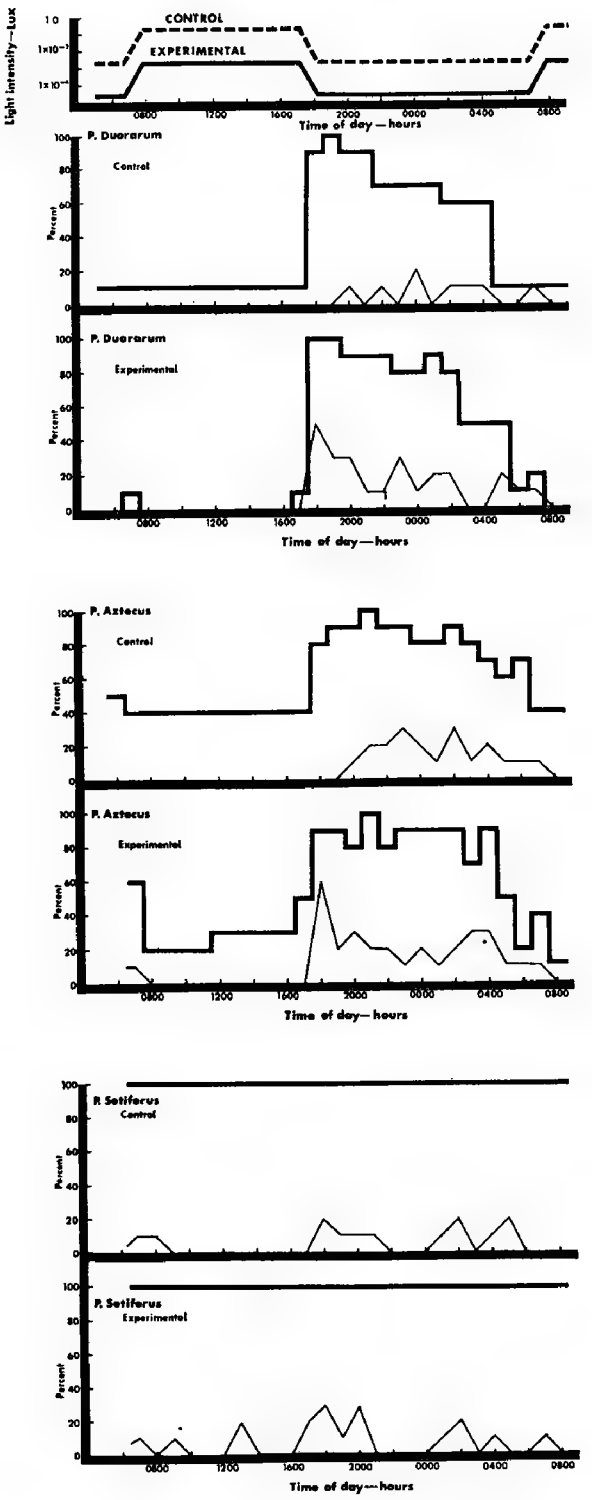

FIG. 6. Activity patterns of *P. duorarum*, *P. aztecus*, and *P. setiferus* on day two under control conditions of L/D 11:13 and 3×10^{-1} to 3×10^{-3} lux, respectively, and experimental low-intensity light cycle conditions of L/D 11:13 and 3×10^{-3} to 3×10^{-5} lux, respectively, in synchrony with environmental day/night. Percent of shrimp exposed shown by histogram and percent swimming activity indicated by line graph.

burrowing were approximately the same for both control and experimental groups. The experimental groups did, however, exhibit some differences in the amount of walking and swimming activity. Pink and brown shrimp activity was nocturnal in both the control and experimental aquaria; however, the activity as indicated by the amount of swimming was greater in the low intensity light experimental aquaria. White shrimp activity in the control aquarium was

greatest during the dim-light regime, while activity in the experimental aquarium occurred continuously.

Activity Patterns with Constant Light

The activity patterns of some species of penaeid shrimp are relatively persistent under constant laboratory environments (Racek 1959; Wickham 1967; Hughes 1968). We observed pink, brown and white shrimp held under constant light for over 50 hr to determine whether these species would maintain their patterns for burrowing and locomotor activity in the absence of cyclic changes in light intensity. The activity patterns obtained during the second cycle under constant light are shown in Figure 7, along with the simultaneous activity pattern of shrimp in the control L/D 11:13 light cycle.

Pink shrimp held under constant light showed a reduction in the number of individuals emerging from their burrows and a suppression in locomotor activity when compared to the same species at the same time in the control aquarium. Emergence and activity under constant light occurred only during the time of environmental darkness and was in phase with the control aquarium dim-light regime. The suppression of activity in pink shrimp in response to constant light was greater than that observed for brown or white shrimp.

Brown shrimp emergence and locomotor activity under experimental constant light were greatest during the time of environmental darkness and were generally in phase with activity in the control aquarium. Experimental brown shrimp were inactive during the time of environmental daylight, although only about half of the individuals burrowed. Activity in brown shrimp held in constant light was concentrated during the noctural hours with occasional swimming occurring about the time of morning and evening twilight. The locomotor activity of brown shrimp was not suppressed to the same extent by the constant light conditions as pink shrimp activity but was more suppressed than white shrimp activity.

White shrimp did not burrow under constant light or the L/D 11:13 cyclic light intensity control conditions. Activity, especially swimming, was suppressed during the time of environmental daylight the first 24 hr under constant light. Activity increased in the experimental aquarium during the nocturnal period of the first daily light cycle and continued with only one brief quiet period near the time of environmental morning twilight at the end of the second cycle. White shrimp activity patterns appeared to be less persistent than those of either pink or brown shrimp, becoming overtly random after approximately 24 hr in either the experimental or control environments.

The amount of activity for all three species, in general, tended to be suppressed under the experimental constant light conditions compared with their respective activity under the control light regime.

Activity Patterns with a 6-hr Light Cycle Phase Advance

The decrease in light intensity associated with evening twilight usually sets the phase for activity rhythms in nocturnal animals (Cloudsley-Thompson

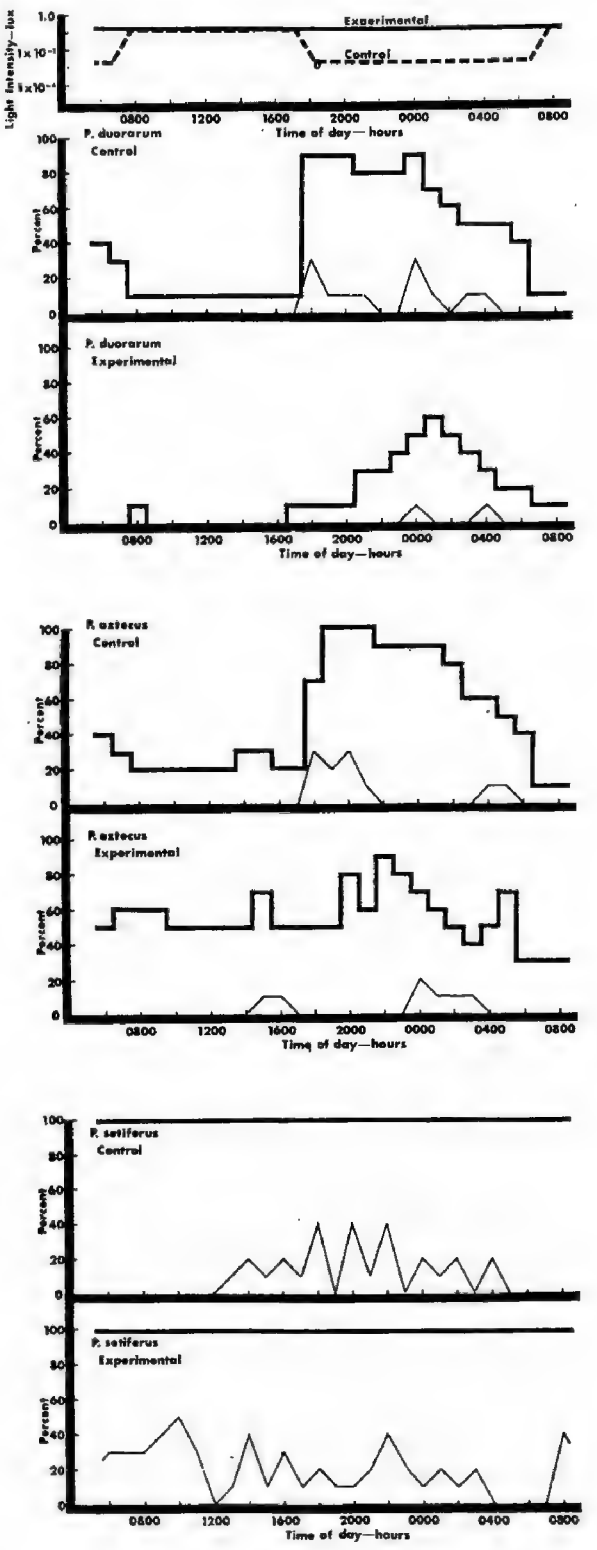

FIG. 7. Activity patterns of *P. duorarum*, *P. aztecus*, and *P. setiferus* on day two under control conditions of L/D 11:13 and 3×10^{-1} to 3×10^{-3} lux, respectively and experimental constant light conditions of 3×10^{-1} lux. Percent of shrimp exposed shown by histogram and percent swimming activity indicated by line graph.

1961). Hughes (1968) provided evidence that for pink shrimp the light/dark transition is the stimulus, or an important component thereof, which maintains the synchrony between the shrimp's internal circadian rhythm and the environmental light/dark cycle.

We subjected pink, brown and white shrimp to an experimental day/night light regime advanced 6 hr (i.e., the experimental aquaria bright/dim transition occurring between 1100 and 1200 hr and the dim/bright transition between 0000 and 0100 hr compared with control aquaria transitions at 1700 to 1800 hr and

0600 to 0700 hr, respectively). This experiment was conducted to observe whether the phase of the circadean activity pattern for each species would be shifted by a 6-hr light stimulus phase advance in relation to the time of environmental day/night, as compared simultaneously to the activity pattern maintained by shrimp in the control aquaria with a L/D 11:13 light cycle in phase with environmental daylight. The experimental shrimp were held preceding this experiment for a period of two daily cycles under a constant light to document the presence and relative overt strength of their endogenous activity component. Results from this experiment are shown in Figure 8.

Pink shrimp in the experimental aquarium responded to the initial decrease in light intensity with at least half of the individuals emerging within one hour following the onset of the 6-hr phase-advanced experimental dim-light regime. The number of shrimp out of their burrows gradually increased during the experimental dim-light regime, reaching a maximum the hour preceding the dim/bright transition. A similar increasing pattern was observed for general locomotor activity. Pink shrimp began to burrow during the dim/bright transition and all were burrowed within one hour following onset of the experimental bright regime. The experimental shrimp activity pattern contrasts with that in the control aquarium where the shrimp were exposed and locomotor activity was at a high level immediately following the dim/bright transition.

The response of brown shrimp to the experimental 6-hr phase advance in the transition to a dim-light regime was similar to the response described for pink shrimp. The most notable difference in the experimental group brown shrimp activity pattern was that 30 to 50 percent of these shrimp, although diurnally inactive, did not burrow during the experimental bright regime. Experimental group locomotor activity, especially swimming, was almost all confined to the dim-light regime. The number of individuals exposed and their amount of activity increased throughout the experimental dim-light regime in a manner similar to experimental group pink shrimp. The general pattern of behavior for brown and pink shrimp in the control aquaria was similar.

White shrimp did not burrow in the experimental or control aquarium. Locomotor activity occurred randomly with no discernible differences in periodicity or responsiveness to light intensity changes in the experimental or control aquarium during the period of the experimental phase-advanced light cycle observations.

DISCUSSION

Shrimp Behavior Observation Methods

Investigators have found it necessary to modify the nocturnal portion of the natural or experimental light cycles to visually observe the nocturnal behavior of shrimp. These modifications to the nocturnal light regime have involved the periodic use of a hand-held flashlight (Fuss 1964) or red filtered light (Fuss & Ogren 1966). A constant dim white light (Wickham 1967) or red light (Hughes 1968; 1969) maintained throughout the nocturnal period is an alternative method for visually observing nocturnal behavior. The latter two methods avoid

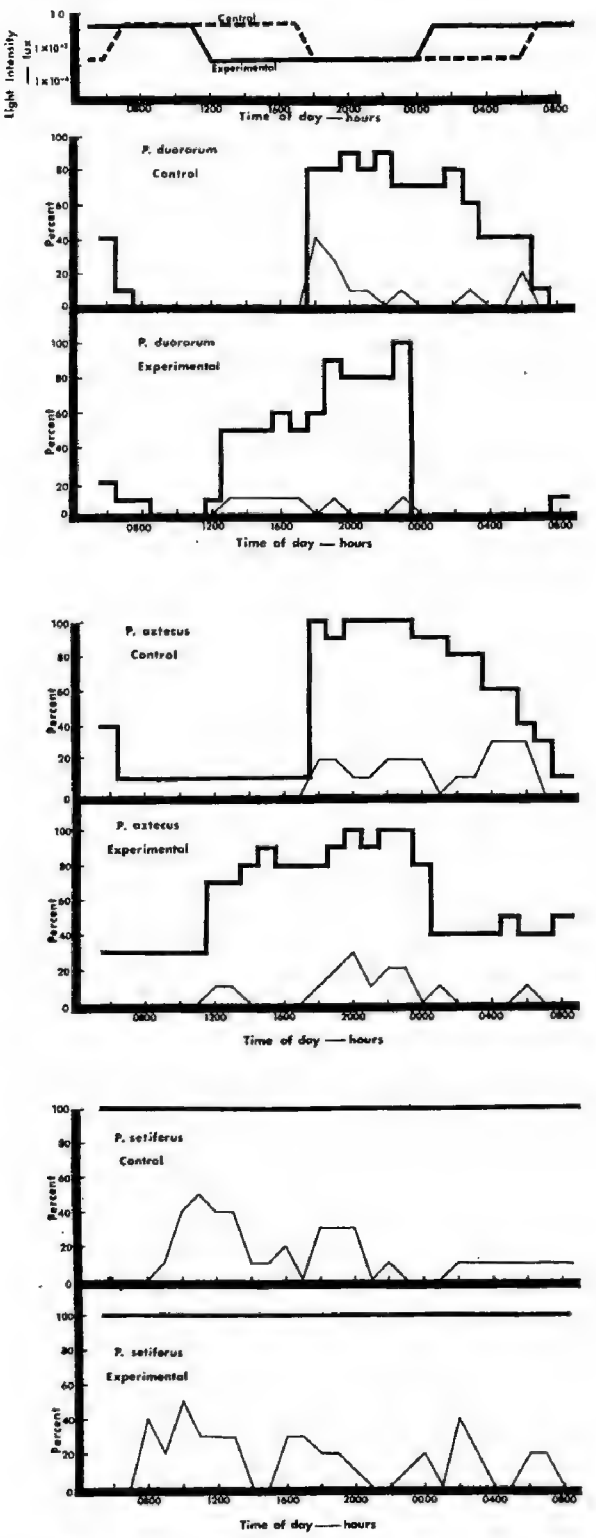

FIG. 8. Activity patterns of *P. duorarum*, *P. aztecus*, and *P. setiferus* under control light conditions of L/D 11:13 and 3×10^{-1} to 3×10^{-3} lux, respectively, in synchrony with environmental day/night and an experimental light cycle identical to the control conditions except advanced six hours in phase relationship to the environment. These observations were initiated following day two under the constant light of 3×10^{-1} lux shown in Figure 7. Percent of shrimp exposed shown by histogram and percent swimming activity indicated by line graph.

intermittent periods of increased light intensity which may, in some animals, stimulate phase resynchronization of the overt rhythmic activity patterns. Short periods of white light (Ogren, ms.), flashed white and infrared light, and strobe light (Klima 1970) have also been used to photograph nocturnal shrimp activities. Klima's study revealed that flashed light did not appreciably affect the pattern of nocturnal behavior for pink shrimp. He observed, however, that a white light (strobe) flash of 0.2-millisecond duration appeared to suppress ac-

tivity levels less than flashed infrared light of 10-sec duration or white light of 3-sec duration.

Our comparison of shrimp behavior, observed visually and with an image intensifier TV-camera system, during the noctural period indicated that constant dim white light of sufficient intensity for visual observation with the dark-adapted human eye apparently did not alter the general pattern of shrimp activity but did tend to suppress the general level of overtly expressed activity. This may be true especially for pink and brown shrimp which appear to be more responsive to changes in light intensity than white shrimp. Our bright-light intensities of 3×10^{-1} and 3×10^{-3} lux with a two order of magnitude intensity reduction (i.e., 3×10^{-3} and 3×10^{-5}, respectively) between dim and bright regimes did not appear to appreciably suppress the activity of white shrimp. These observations indicate that constant dim white light of sufficient intensity for dark-adapted human vision can be used for observing nocturnal shrimp behavior with the awareness that, depending on the animal's sensitivity to light, activity may be suppressed such that only motivational peaks of activity are overtly expressed. Comparative observations were not made to evaluate whether shrimp activity might be less affected by narrow-band specteral composition light of sufficient intensity for human visual observations than by dim white light.

Effects of Light on Activity Patterns

Our experimental results indicate differences exist among the normal patterns of burrowing and locomotor activity exhibited by pink, brown and white shrimp and also in the degree of their responsiveness to light and the persistence of a synchronized rhythmicity in their activity patterns. A comparison of the burrowing and locomotor behavior exhibited by these three species suggests a gradation exists in the degree of their sensitivity or responsiveness to light stimuli. Pink shrimp were the most responsive to the various changes in the experimental light stimuli. Brown shrimp responded to light slightly less than pink shrimp, as a greater percentage of individual shrimp did not always respond to the experimental changes in light stimulus. White shrimp were the least responsive to our experimental light-cycle alterations, although some suppression in activity was indicated during the initial day of a control intensity bright-light regime. The sensitivity of a shrimp species to diel light intensity changes may be related to their preferred ecological habitats and the water clarity in these areas (Lindner and Bailey 1969). The distribution and ecological preferences of pink, brown and white shrimp were described by Springer and Bullis (1954), Williams (1958), Perez-Farfante (1969) and Grady (1971). Light sensitivity differences may also be influenced by the drive state of each species associated with the seasonal timing of their respective maturation and offshore migration from the estuaries.

Activity Patterns and Shrimp Availability to Fishing Gear

The patterns of shrimp activity resulting from light intensity changes and endogenous factors may directly affect a shrimp's availability to capture with

conventional harvesting methods and gear by influencing the time of day and duration of burrowing, activity on or near the substrate and swimming in the water column. The behavior of shrimp during their diurnal or nocturnal activity periods may also be influenced by factors such as tidal rhythms (Hughes 1969). The diurnal burrowing of pink and brown shrimp reduces their availability to conventional shrimp trawls. Ogren (ms.) obtained *in situ* observations of the diurnal burrowing behavior of white shrimp in St. Andrews Bay, Panama City, Fla., which were comparable to the burrowing behavior of pink shrimp; while Williams (1958) reported that white shrimp burrow, but not with the regularity or to the extent exhibited by pink and brown shrimp. These observations by both Ogren and Williams reveal that white shrimp will burrow diurnally under the proper environmental conditions. Our observations indicate, however, that diurnal availability of white shrimp to fishing gear might result from limited activity and quiescent periods on the substrate surface. Fishing for white shrimp, in fact, is normally conducted during the daytime.

Swimming activity may also reduce the availability of shrimp to capture with bottom trawls by carrying the shrimp up into the water column to heights above that of a trawl headrope. The periods of nocturnal swimming activity that occurs in pink and brown shrimp could reduce their availability to capture with a trawl; however, much of their activity appears to be associated with the substrate. Shrimp on or near the substrate are vulnerable to capture with a conventional bottom trawl. White shrimp are more active and swim considerably more than the other two species. A high level of nocturnal swimming by white shrimp could result in their spending much time in the water column and possibly account for reports from fishermen of a reduction in white shrimp in their trawl catches after dark.

ACKNOWLEDGMENTS

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CAUSES AND PROBABLE CORRECTIVES FOR OXYGEN DEPLETION FISH KILLS IN THE DICKINSON BAYOU ESTUARY: A FIELD STUDY AND SIMPLIFIED ALGAL ASSAY

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ABSTRACT

Frequent oxygen depletion fish kills, caused by dense algal blooms, have occurred during summers in the six-kilometer portion of Dickinson Bayou directly upstream from two sewage treatment plants. These plants are the major contributors of wastes to the bayou. During summer periods of low freshwater inflow, the treatment plant effluents are carried upstream by tidal action, causing dense algal blooms; algal density is much less above tidal influence and downstream from the plant outfalls. Algal assays demonstrated that if the plants employed chemical coagulation to remove phosphorus, the summer algal densities in the critical six-kilometer portion of the bayou would be reduced to concentrations corresponding to, or less than, the levels found in the rest of the bayou. Such treatment would thereby reduce the probability of summer fish kills.

INTRODUCTION

Man's activities, which introduce excess nutrients into bodies of water, can adversely effect the aquatic environment. The artificial addition of nutrients accelerates the process of eutrophication and leads to increased algal growth. The consequences of hyper-eutrophication are usually unpleasant and solutions to the problem are often complex and difficult to attain.

In the coastal areas of Texas, where population and industrial development are increasing at a rapid rate, the problem of eutrophication is becoming a serious one. Our department investigated 48 eutrophication-related fish kills during 1971 and 1972, all in the Houston-Galveston area. Recurring kills were investigated in some of the small, shallow, tidal streams, or bayous, during periods of light rainfall. One such bayou was Dickinson Bayou, located in Galveston and Brazoria counties, Texas, where it meanders some 36 kilometers from its source near Alvin to its confluence with Galveston Bay (Fig. 1).

Dickinson Bayou has a watershed of 106 square miles (275 km^2) which is drained by seventeen small tributaries. Most of the tributaries carry only rainfall runoff. The land in the watershed is used primarily for livestock grazing and for the farming of rice, soy beans, milo, corn and sweet sorghum. The principal

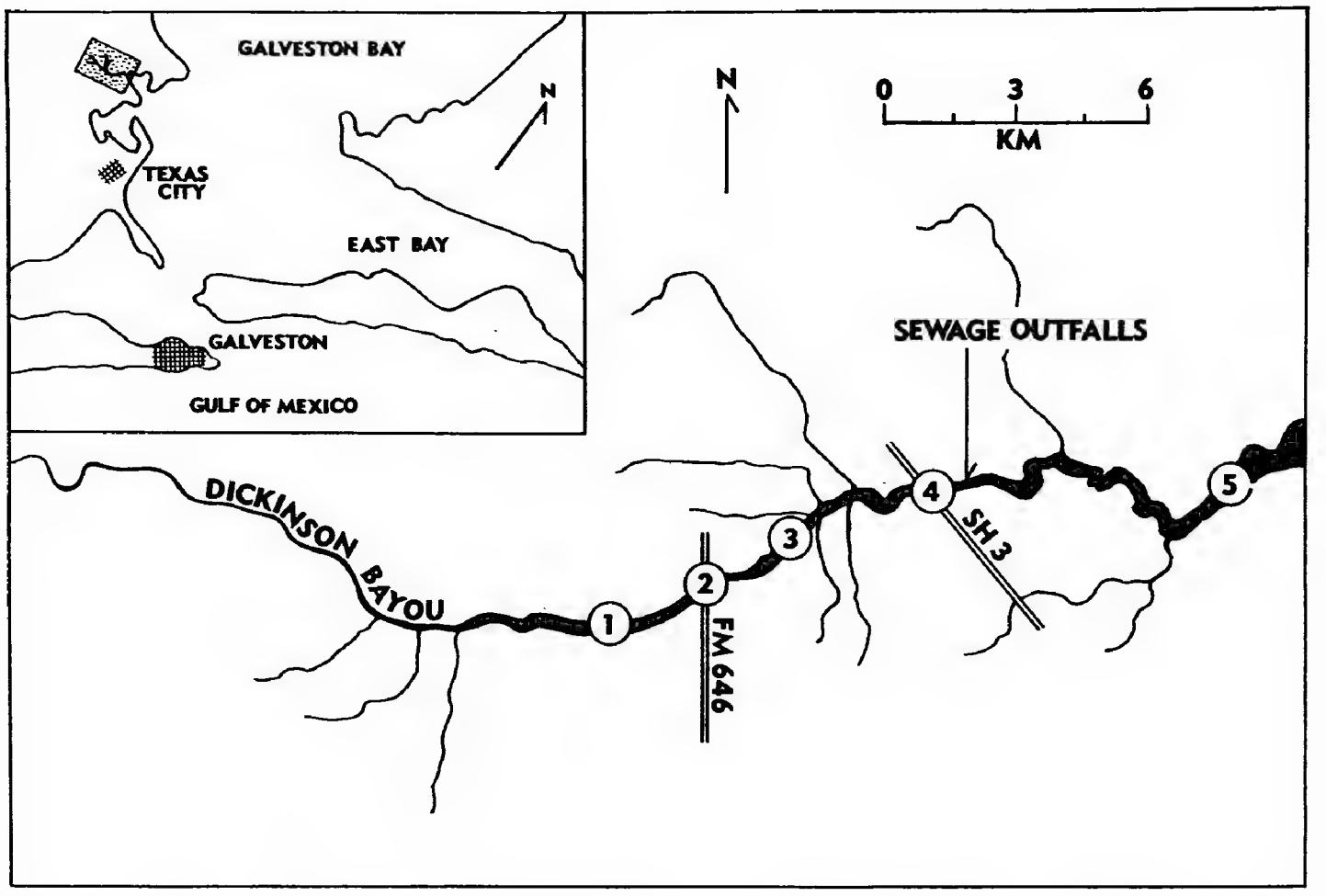

FIG. 1. Map of Dickinson Bayou with the locations of the sewage treatment plant outfalls and sampling stations.

residential and commercial development along the bayou is in and around the unincorporated town of Dickinson, which has a population of 14,000. The area has a mild climate with an average winter temperature of 53 F (11.7 C), an average summer temperature of 83 F (28.3 C) and an annual mean temperature of 69 F (20.6 C). The average annual rainfall in the watershed is 45 to 50 inches (114–127 cm). Kirkpatrick (1972) provides a very detailed description of the area.

Dickinson Bayou is used for recreational fishing, canoeing, swimming and water skiing. Saline water intrudes nearly halfway up the bayou during dry weather, providing salt water fishing, crabbing and shrimping as additional recreation. But, according to long time residents, the aesthetics of Dickinson Bayou have deteriorated in recent years. During the warmer months floating mats of algae are present and fish kills are frequent. In 1971 our department investigated five fish kills in the bayou and estimated that over four million fish were destroyed. These fish kills, and a large kill in July, 1972, were concentrated in the area of Dickinson Bayou between State Highway 3 (SH 3) and Farm to Market Road 646 (FM 646) (Fig. 1). The cause of all these fish kills was attributed to low dissolved oxygen concentrations.

The normal diel fluctuation of dissolved oxygen is disturbed by two principal factors: (1) the addition of industrial, agricultural and domestic wastes which are available for biological and chemical oxidation, and (2) "blooms" of algae, which supersaturate the water with oxygen during the day through photosyn-

thesis and deplete the oxygen at night through respiration. In Dickinson Bayou, the most damaging of man's activities appears to be the introduction of domestic waste. Only two small industries discharge into the bayou, and agricultural run-off usually occurs during periods of heavy rainfall in spring and autumn. In contrast, two domestic treatment plants, located along the bayou within two kilometers of each other, discharge nearly two million gallons (7571 m^3) of wastewater per day. Both plants provide secondary treatment and have no facilities for nutrient removal.

Early in 1972, the larger of the two sewage treatment plants announced plans to increase the volume of its 1.2 million- gallon (4542 m^3) per day discharge. Because of these expansion plans, we conducted a field study of Dickinson Bayou from April through August of 1972 to determine what factors were likely causing a disturbance in the oxygen balance of the stream, particularly between SH 3 and FM 646, where the numerous fish kills have been concentrated. We wanted to determine if the sewage treatment plants' effluents contributed to the algal blooms and fish kills, since they were immediately downstream from this area. Once we suspected that the plants might be an influence, we conducted laboratory algal assays to determine if advanced treatment for phosphorous removal might alleviate the majority of the water quality problems in the bayou.

FIELD STUDY

Methods

Five stations on Dickinson Bayou were sampled weekly from 20 April through 31 August, 1972. Three stations were within the area of frequent fish kills, with one station above and one station below this area (Fig. 1). The sewage treatment plants' effluents were sampled monthly for total phosphorous. Surface and bottom salinity, dissolved oxygen and temperature were measured in the bayou. All samples were collected at mid-stream between 9:00 A.M. and 11:30 A.M. on each date. Surface values for total phosphorous and chlorophyll-*a* were also determined beginning in the first week of July, when saline water became detectable on the botton at all three stations within the area of the fish kills. To estimate the phosphorous content of incoming tidal waters, weekly surface samples for total phosphorous analysis were collected from the mouth of the bayou between 7 July and 31 August, 1972. Salinities were measured with a Goldberg Model TC Refractometer. The azide modification of the Winkler Method was used for dissolved oxygen measurements. Phosphorous samples were separated into dissolved and suspended fractions by filtering the samples through a 0.45 micron Millipore filter. The samples were then digested using persulfate oxidation, followed by the ascorbic acid technique for the final colorimetric determination (Amer. Public Health Ass. 1971.).

Since chlorophyll-*a* limits the rate of photosynthesis (Holmes 1968), and can usually be directly related to plant biomass (Odum 1959), this pigment was measured as a rough index of algal standing crop. Chlorophyll-*a* was determined by the technique of Odum, McConnell and Abbott (1958). After filtering the sample through a 0.45 micron Millipore filter, the filter and residue were dissolved in 90% acetone and kept in the dark at 4 C for twenty-four hours. To determine the chlorophyll-*a* concentration, the optical density of the acetone extract was measured on a Bausch and Lomb Spectronic 20 at a wave length of 665 mμ.

Results

In April and May, due to heavy rainfall, freshwater runoff dominated the bayou's circulation. Salinity values were negligible, while the dissolved oxygen

content of surface and bottom waters was near saturation at all sample stations. As the rain decreased in June, saline water began to intrude upstream, first on the bottom, then on the surface. Only a small amount of mixing occurred between the surface water and the more dense saline layers, resulting in very low dissolved oxygen concentrations on the bottom (Fig. 2). Precipitation and surface runoff into the bayou continued to be negligible in July and August, and tidal action dominated circulation (Fig. 3).

Ketchum (1971) stated that a pollutant is carried upstream in an estuary to the same extent that salt is carried upstream, and by the same mechanism. To show that this type of tidal transport system functions in Dickinson Bayou, surface phosphorous samples were collected weekly in July and August (Fig. 4). The highest phosphorous concentration was found at the station nearest the sewage treatment plants, decreasing upstream in proportion to decreasing salinity ($p < 0.01$, for the product-moment correlation between surface phosphorous and salinity concentrations; $r = 0.76$ with 23 degrees of freedom). The average total phosphorous concentration of incoming tidal waters, found by sampling the mouth of the bayou in July and August, was 0.325 mg/l, with a range from 0.47 mg/l, on August 31, to 0.20 mg/l on July 7. The phosphorous levels at the "affected" stations, stations 2 through 4, differed significantly from those at "unaffected" station 1 ($p < 0.01$, using the *t*-test for paired observations with 7 degrees of freedom) and from those measured at the bayou's mouth ($p < 0.05$,

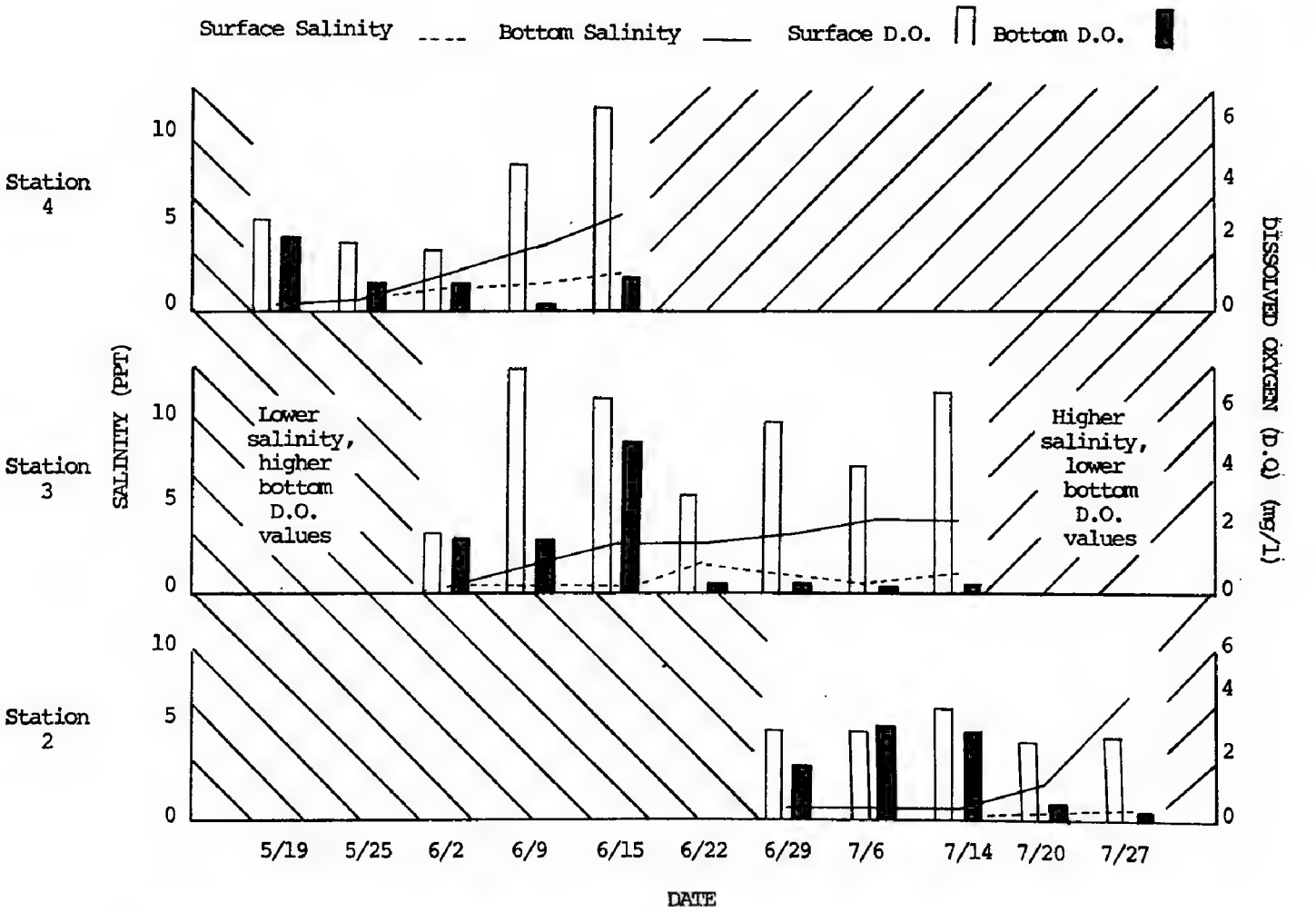

FIG. 2. Salinity and dissolved oxygen values for selected dates at stations 2, 3, and 4, showing the upstream movement of saline water with its low dissolved oxygen content.

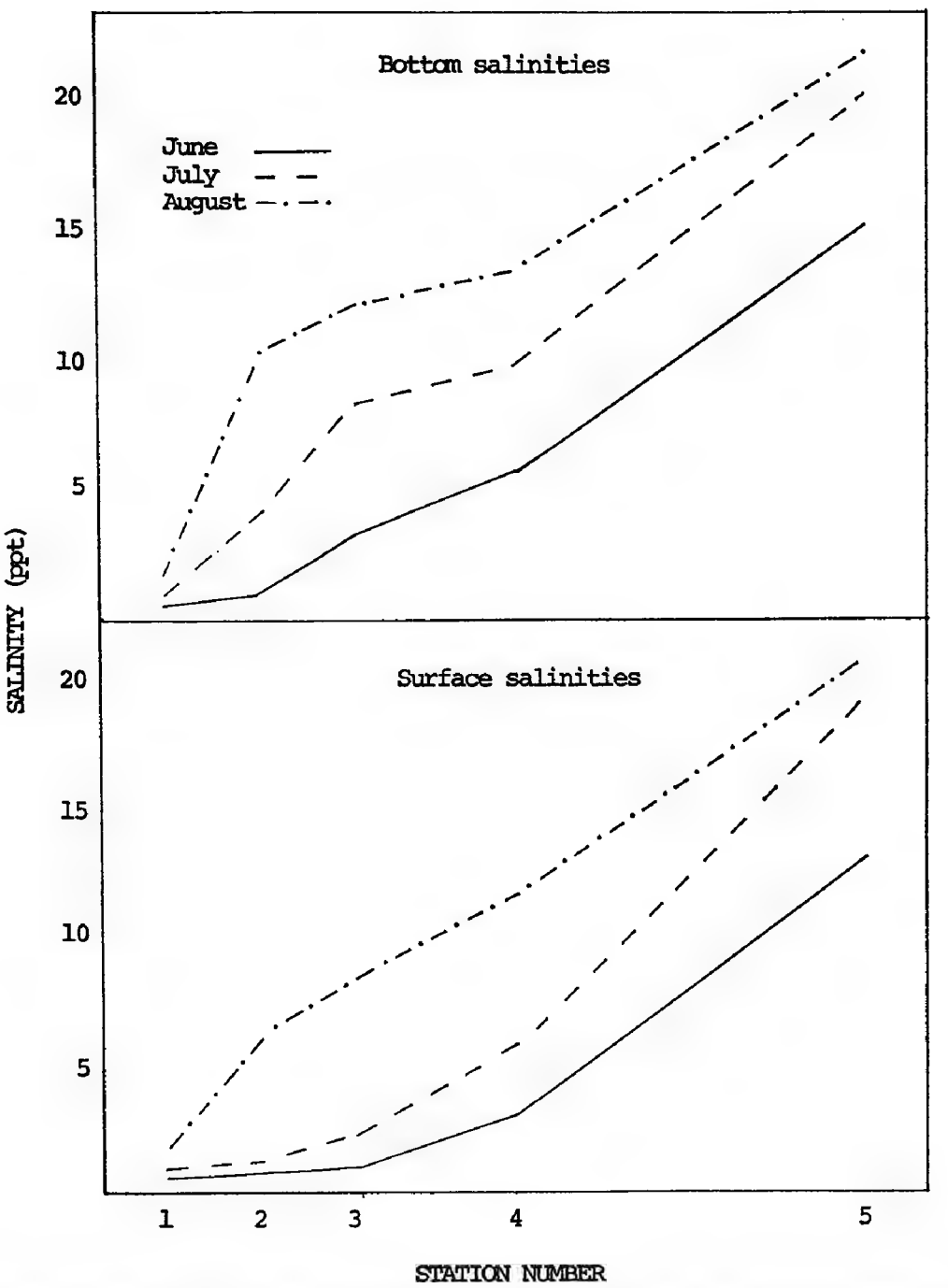

FIG. 3. Monthly station averages for salinity on the surface and the bottom. Distances are to scale along the x-axis.

using the *t*-test for paired observations with 7 degrees of freedom). The highest chlorophyll-*a* concentrations were found in the same segment of the bayou as were the highest total phosphorous concentrations, i.e., stations 2 through 4 (Figure 5). The chlorophyll-*a* levels at stations 1 and 5 were significantly different from those at stations 2, 3 and 4 ($p < 0.05$, using the *t*-test for paired observations with 7 degrees of freedom).

Since the area between stations 2 and 4 was the focal point of frequent fish kills, a cause-and-effect relationship between algal density and oxygen balance was evaluated. On August 17, the chlorophyll-*a* value for stations 4 and 5 were 0.48 mg/l and 0.31 mg/l, respectively. These values represented the densest algal concentrations found at each during the study. Dissolved oxygen concentrations were determined over a twenty-four hour period, at three-hour intervals, beginning at noon on August 17. The dissolved oxygen range fluctuated 13.4 mg/l at station 4 compared to 6.5 mg/l at station 5 (Fig. 6). Extreme diel

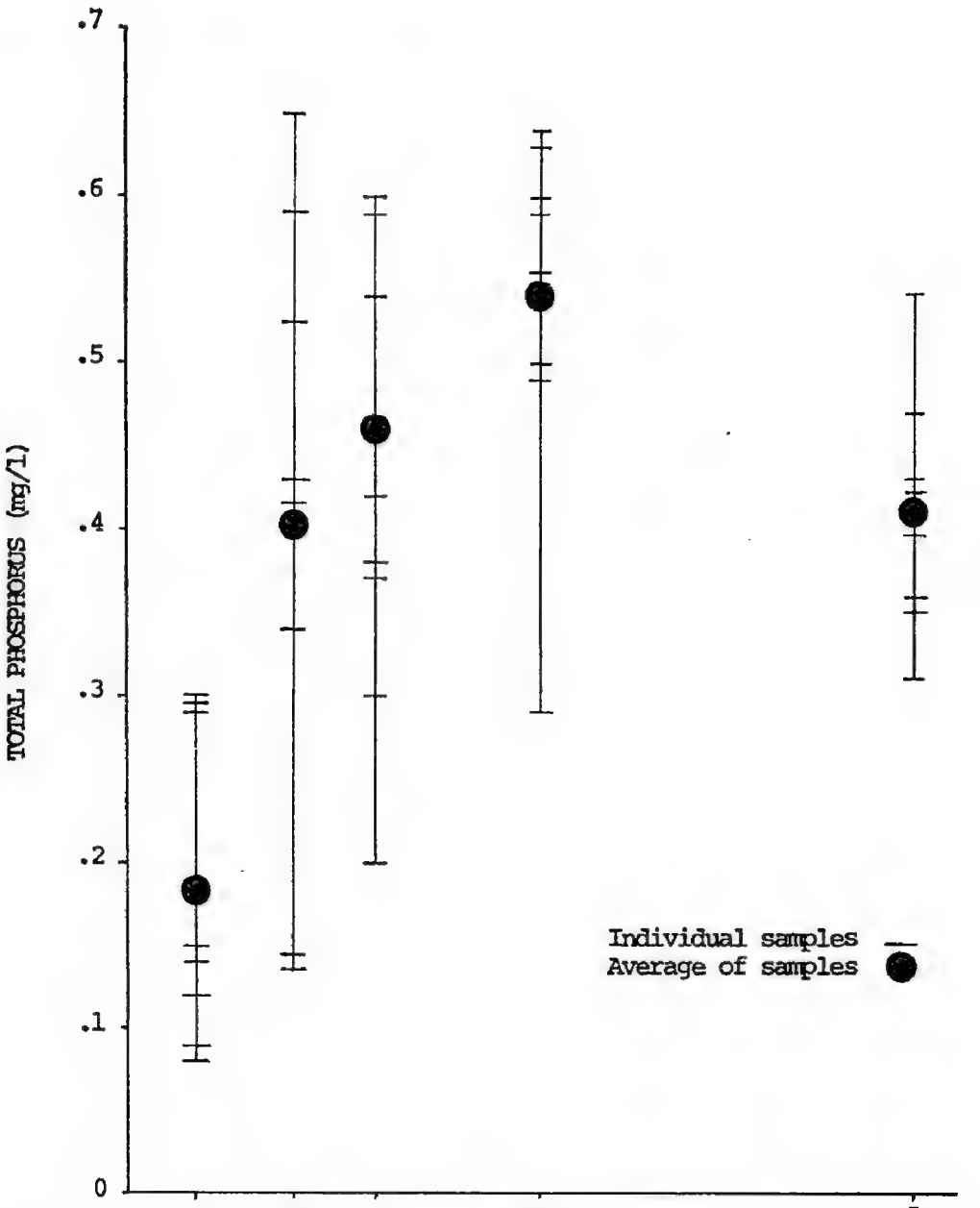

FIG. 4. Individual samples and averages for total surface phosphorus concentrations at each station in July and August, 1972. Distances between stations are to scale along the x-axis.

fluctuations in dissolved oxygen in Dickinson Bayou can be attributed to algal density, since the incident solar radiation, vertical mixing or wind, would be nearly equal throughout all of the stations. As shown by the chlorophyll-*a* data in Figure 5, algal populations capable of producing extreme dissolved oxygen fluctuations, such as occurred at station 4 on August 17, were present on at least five occasions at stations within the area of frequent fish kills, but never at the other "unaffected" stations.

Monthly total phosphorous analyses on the effluents from the sewage treatment plants showed that the average phosphorous concentration at the larger plant was 11.1 mg/l, with levels ranging from 9.6 mg/l in April to 14.2 mg/l in July. The smaller plant's discharge averaged 10.2 mg/l of total phosphorous, with a low value of 8.8 mg/l in April and a high value of 12.7 mg/l in August. Scudday and Nichols (1972) calculated that if the larger treatment plant reduced its effluent's total phosphorous concentration to 1.0 mg/l, then the resulting "dry

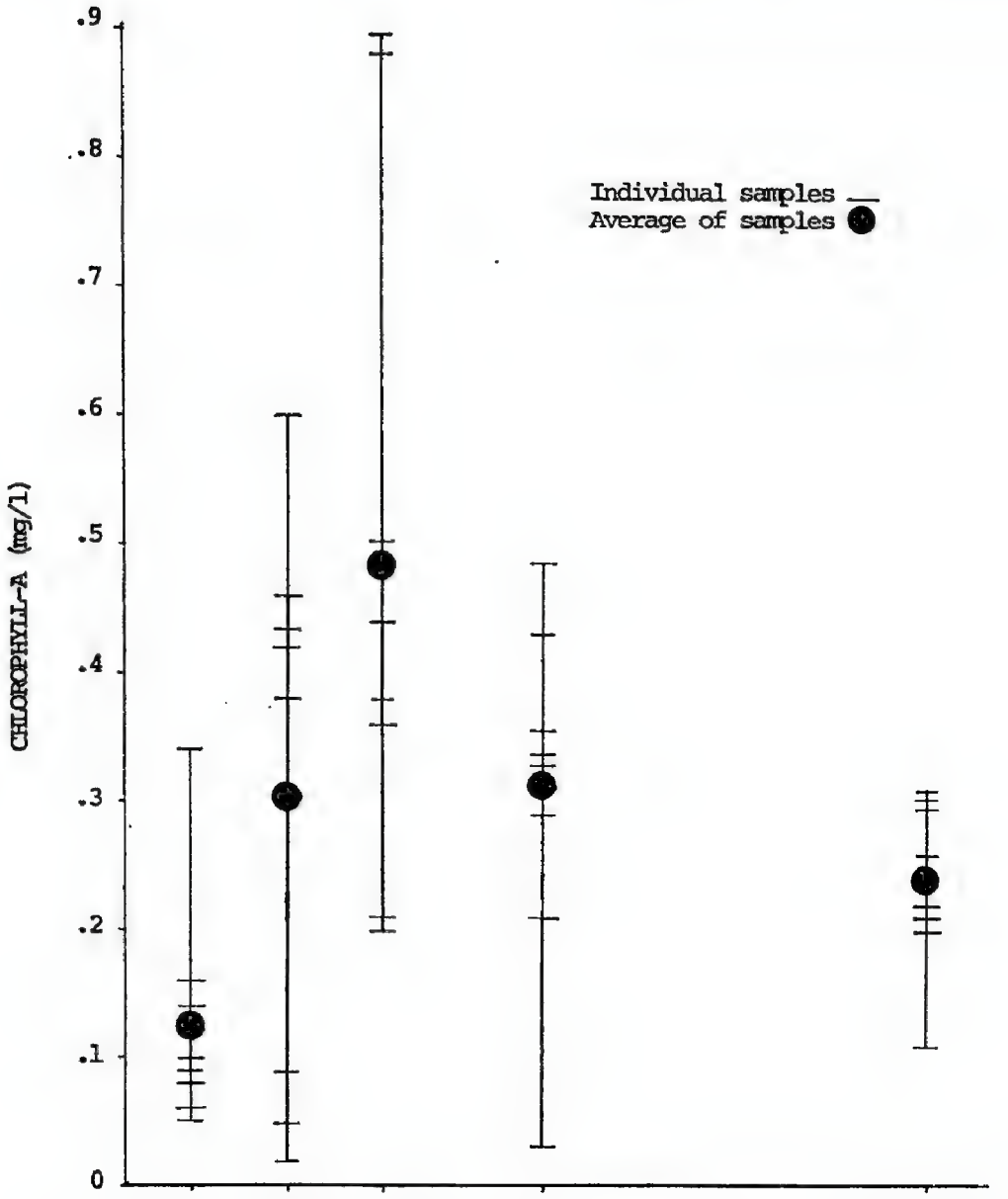

FIG. 5. Individual samples and averages of samples for surface chlorophyll-*a* concentrations at each station in July and August, 1972. Distances between stations are to scale along the x-axis.

weather" phosphorous load in Dickinson Bayou would be reduced by 70%. Their estimate took into account all known phosphorous-containing inflows to the bayou.

ALGAL ASSAYS

Methods

Since enrichment by secondary sewage effluent was shown to contribute to the cause of algal blooms in Dickinson Bayou, it was left to be demonstrated if advanced treatment for phosphorous removal would help reduce algal populations. Phosphorous rather than nitrogen removal was advocated as the preferred form of advanced treatment for several reasons: (1) the algal community in Dickinson Bayou often contained a large percentage of blue-green algae; Thomas (1971) found that the addition of phosphorous alone to water is sufficient to increase the growth of this type of algae, (2) blue-green algae are able to bind gaseous nitrogen organically, thereby producing nitrates and nitrites for green algae; Shapiro and Ribeiro (1965) have shown that the increased growth of blue-gree algae with available phosphorous may even supply enough nutrient nitrogen to produced blooms of green algae, (3) out of the putrified parts of organisms

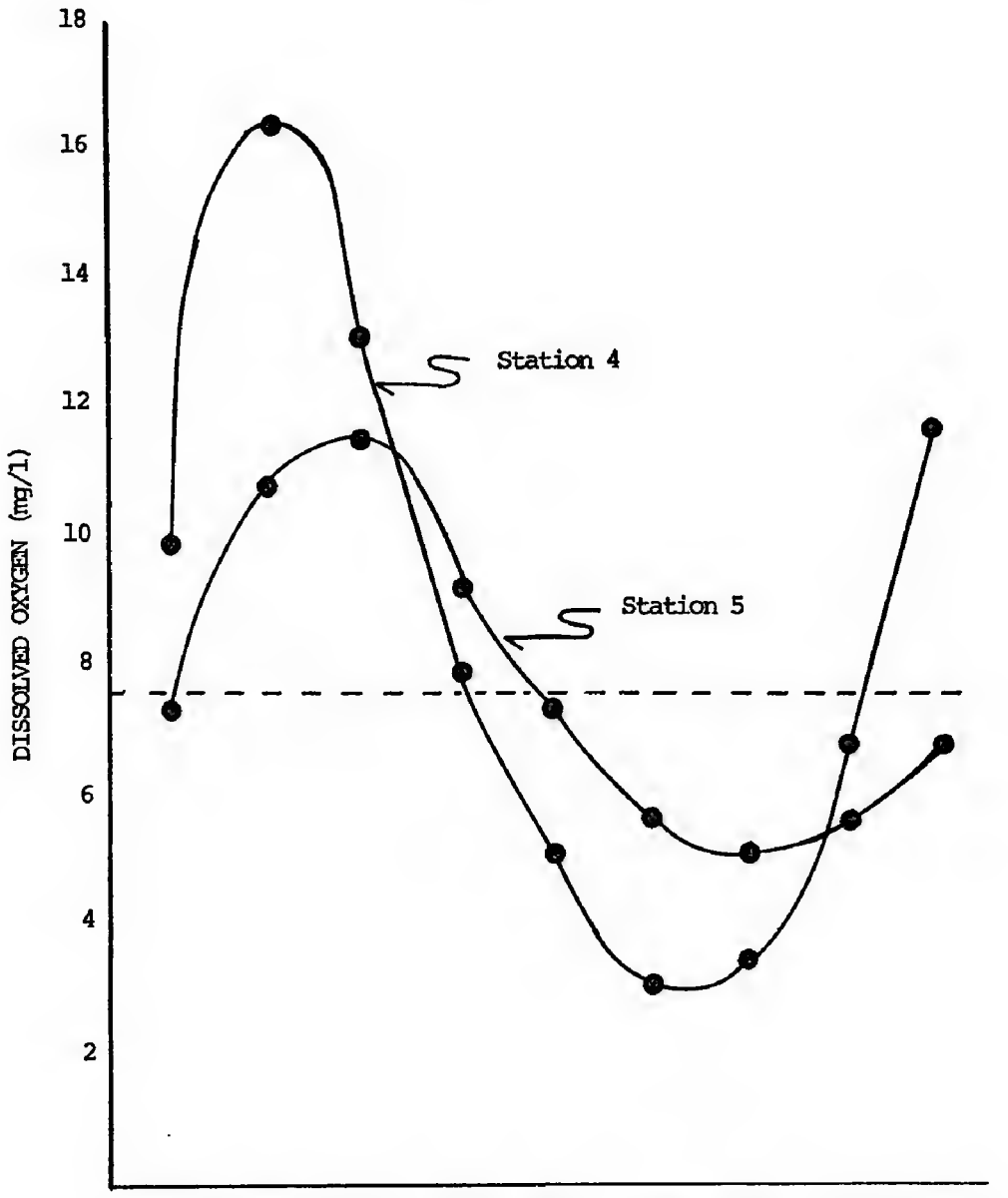

FIG. 6. Diel fluctuations in dissolved oxygen at stations 4 and 5 on August 17 and 18, a time of the highest chlorophyll-*a* concentrations at both stations during the study period. The dashed line indicates the normal saturation value for dissolved oxygen at the temperature and chloride values encountered during the twenty-four hour period.

and sludge, nitrogen compounds return in larger quantities than phosphorous compounds in the biochemical cycle (Thomas 1971), and (4) in the industralized areas of the Texas Gulf Coast, numerous industries produce ferric chloride and alum as by-products, providing a cheap and ample source of these compounds for sewage treatment plants to use for the coagulation of phosphorus.

Algal assays were conducted to demonstrate the benefits of using advanced treatment for phosphorus removal. The use of such algal growth tests has increased in recent years as a tool to help control eutrophication. Most of the assays now in use, including the test developed by the Joint Industry/Government Task Force on Eutrophication (United States Environmental Protection Agency, 1971), employ unialgal cultures, spiked with various combinations of nutrients, with the intent of determining which nutrient or nutrients are limiting to the growth of a specific algal species in a particular body of water. These tests usually require several replicates of each possible limiting nutrient, several culture media preparations, and strict measures to avoid bacteriological and chemical contamination. Even when a waste effluent is to be evaluated, the same procedures and precautions must be followed. In this study we used an assay that does not define a limiting nutrient *per se*, but does indicate how the algal population of a receiving

stream will respond to a particular sewage effluent. Here, the test was used to determine if there were any significant differences in algal growth between solutions of Dickinson Bayou water mixed with secondary sewage and bayou water mixed with actual and simulated tertiary sewage (phosphorous significantly removed by chemical coagulation). This assay procedure does not require elaborate laboratory facilities.

Algal assays were conducted beginning on 30 August, 1972, and again on 9 April, 1973. On the day prior to the tests, bayou water was collected from station 5 and secondary sewage effluent was collected from the larger plant on Dickinson Bayou. All water samples were filtered through Reeve Angel 1934 AH filter paper to remove the suspended solids. A portion of the Bayou water was kept unfiltered for use as a mixed phytoplankton seed. For the first assay, tertiary effluent (phosphorous substantially removed) was collected from the Houston Lighting and Power Company domestic waste treatment plant at Webster, Texas. This plant employs chemical coagulation and filtration and removes over 95% of the total influent phosphorous. For the second assay, phosphorus was removed from the secondary effluent in the laboratory, using the same coagulation process that is used at the Webster plant—$Al_2(SO_4)_3 \cdot 18H_2O$ was added to the secondary effluent and NaOH was used to neutralize the treated effluent.

To begin the assays, 200 ml solutions containing percentages of the sewage effluents with Dickinson Bayou water were placed in 300 ml erlenmeyer flasks. The dilutions of the effluents in the bayou water were chosen in accord with dilutions expected in actual practice. The volume of Dickinson Bayou from the sewage treatment plants upstream to FM 646 is approximately 90 million gallons ($341 \times 10^3 m^3$) (Texas Water Quality Board, unpublished). Assuming that the downstream flow of the bayou is negligible and that the sewage treatment plants discharge 2.0 million gallons (7571 m^3) per day, tidal action, by moving the effluent upstream, could cause this segment of the bayou to become as much as 50% sewage in 45 days. So, dilutions of 50, 30, 10, 5, and 0% sewage in bayou water were evaluated in the assays to represent the more extreme and less extreme conditions. A duplicate of each solution was prepared. Five milliliters of well mixed unfiltered Dickinson Bayou water were added to each solution to provide a mixed phytoplankton population as seed. The flasks were stoppered with cotton and placed on a three square foot surface within a Marsh Instruments Model 805 incubator. Two 15 watt fluorescent lamps with reflectors were placed above the flasks. To simulate summer conditions, the lamps were cycled on and off for 14 hours and 10 hours, respectively, and the temperature of the incubator was kept at 27 ± 1 C. During the assays the flasks were swirled daily to provide adequate CO_2 exchange. The positions of the flasks were altered daily to insure even light distribution.

The maximum standing crop, after a given period of time, was used to evaluate the growth of the algal populations. The first assay was concluded after 21 days. The algal mass in each flask was thoroughly mixed and the chlorophyll-*a* of the suspensions was determined. The second test was concluded after 23 days. For this assay the total suspended solids, rather than chlorophyll-*a* was used to measure algal biomass. This change in procedure was made because total suspended solids provides a more direct measurement of biomass. Microscopic examination of the algal cultures showed that algal forms were the dominant organisms, and that no zooplankters or other animal forms were present. At the beginning of this assay, the initial total suspended solids in each flask was negligible; therefore any weight increase was attributed to algal growth. To measure the suspended solids, a portion of each well mixed algal suspension was filtered through a pre-weighed 0.45 micron Millipore filter and dried overnight at 75 ± 2 C prior to weighing to ± 0.1 mg on an analytical balance.

Results

In the first algal assay, the total dissolved phosphorous concentrations of the secondary sewage effluent, tertiary effluent, and Dickinson Bayou water were 7.65 mg/l, 0.22 mg/l and 0.33 mg/l, respectively; in the second assay these same values were 8.91 mg/l, 0.35 mg/l and 0.14 mg/l. In both assays, the secondary

sewage effluent produced more algal biomass when added to the bayou water than did the bayou water alone. The dilutions of the secondary effluent also produced more algal biomass than did equal dilutions of the tertiary effluent (Fig. 7). The first assay did not give the same "stair-step" reduction in algal growth which was attained in the second assay. The results of the former assay, however, were reported as chlorophyll-*a* rather than as total suspended solids. Considering the small volumes involved and possible bleaching of chlorophyll-*a* during the assay (Shapiro and Ribiero 1965), total suspended solids was considered a more accurate parameter for evaluating the algal biomass. In the second assay the tertiary effluent gave a two- to four-fold reduction in algal growth over similar dilutions of secondary effluent.

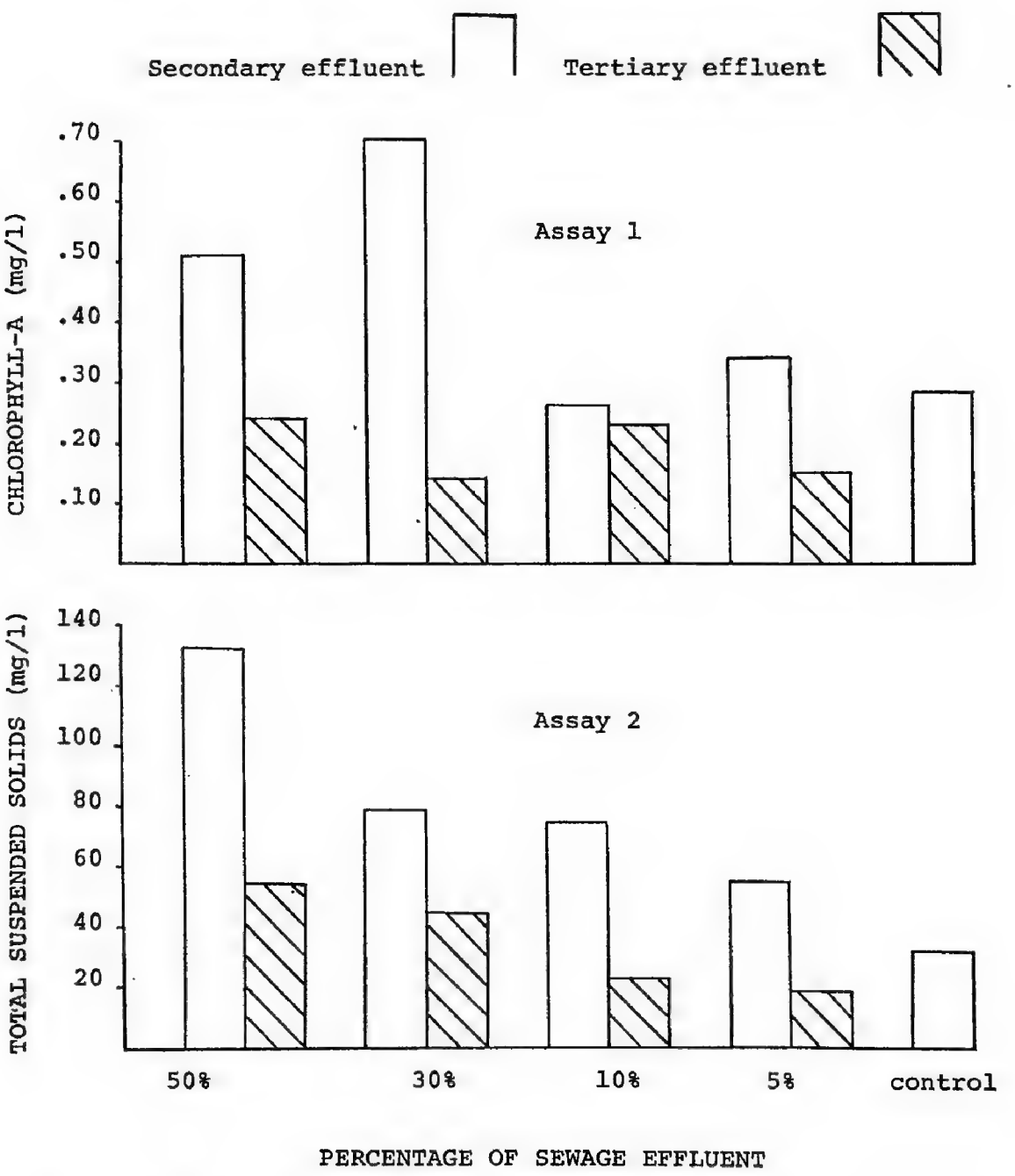

FIG. 7. Results of two laboratory algal assays, which compared the growth of mixed algal populations at equal percentages of secondary sewage effluent versus tertiary sewage effluent, in combinations with Dickinson Bayou water, showing the biomass reductions achieved with the latter treatment.

DISCUSSION AND CONCLUSION

The oxygen balance of Dickinson Bayou is upset by a combination of natural and man-caused influences. The low dissolved oxygen content of bottom waters during salt water intrusion is a characteristic of narrow, vertically stratified estuaries. This natural effect, by itself, is an unlikely cause of fish kills, since most organisms can avoid bottom waters. The intermediate and surface waters of stratified estuaries normally contain sufficient dissolved oxygen concentrations, unless disturbed by man. In Dickinson Bayou the two sewage treatment plants contribute nearly all of the wastes to the bayou during summers; and as determined by the field study, these wastes influence the affected portion of the bayou.

All of the major fish kills in Dickinson Bayou during 1971 and 1972 occurred during the night or early morning, and during significant algal blooms. The physical reaeration potential of the five km section of the bayou directly upstream from the two sewage treatment plants was estimated by Kirkpatrick (1972). He found that the BOD loading by the plants would reduce the dissolved oxygen to levels below 4.0 mg/l on less than 5% of the critical summer days. It therefore appears that the algal-stimulating nutrients in the sewage treatment plant effluents, rather than the oxygen demanding wastes, are the primary cause of the disturbance of the oxygen balance in the bayou from the area of SH 3 to FM 646.

Algal assays demonstrated that, in the critical six kilometers of the bayou above the sewage treatment plants, advanced treatment for phosphorous removal would likely reduced the algal standing crop to a level of one half, and possibly as little as one quarter, of past summer densities. This reduced standing crop would then be equal to, or less than, that which is normally present in summers at stations above and below the area of frequent fish kills. This algal biomass reduction could thus eliminate the extreme diel dissolved oxygen fluctuations in the affected portions of the bayou and greatly reduce the likelihood of summer fish kills.

Considering the algal assay results and the estimate that phosphorous removal to a level of 1.0 mg/l would reduce the phosphorous loading by 70%, it appears that phosphorous removal could alleviate the dissolved oxygen problems in Dickinson Bayou. In fact, the state regulatory agency over domestic waste discharges, the Texas Water Quality Board, has ordered the larger treatment plant to implement phosphorous removal. When the plant begins removing phosphorous from its effluent, another study should be conducted to determine if the conclusions of this study are indeed valid. Such a study would be helpful in determining how similar problems should be approached in the future; and if it is found that phosphorous removal significantly improves the situation, the availability of low cost chemical by-products for the removal of phosphorous would offer a relatively easy and inexpensive means for correcting other eutrophication problems.

Further, Kirkpatrick (1972) concluded that the sewage treatment plants on Dickinson Bayou were poorly located, because the area into which they discharge is "normally stagnant, highly eutrophic, unstable and typically supports no benthic organisms." The results of our field study support this conclusion. When

planning and selecting sites for future sewage treatment plants in tidal streams, the build-up of nutrients, which lead to algal blooms and fish kills, should be considered.

ACKNOWLEDGMENTS

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SEASONAL VARIATIONS IN NEARSHORE CIRCULATION IN THE NORTHWESTERN GULF OF MEXICO

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ABSTRACT

Sub-surface current data from a late winter and a midsummer period are used to describe the nearshore circulation in the northwestern Gulf of Mexico. The winter currents are generally west-southwesterly and average approximately 21.5 cm/sec. The summer currents alternate between a south-southwesterly and a north-northwesterly direction with little net transport. Comparison of simultaneously collected wind and current data suggests that many features of the nearshore current patterns can be explained as a response to surface windstress.

INTRODUCTION

Circulation studies in the northwestern Gulf of Mexico have for the most part utilized drift bottle data or involved the compilation of ship drift calculations. Historical ship drift data, summarized in U. S. Hydrographic Office charts (see Leipper 1954), suggest the existence of a surface convergence near latitude 27°N (see Figure 1). Much of the work over the past twenty years has been aimed at defining the temporal and spatial characteristics of this convergence along the Texas continental shelf as a response to the overlying wind field.

Geological evidence in the form of heavy mineral distributions (Bullard 1942, Van Andel and Poole 1960), sand size modes (Hayes 1965) and the longshore distribution of shell material (Watson 1968) all support the idea of a convergence in the littoral drift along central Padre Island. Drift bottle studies conducted over the inner continental shelf over the past ten years are in general agreement; however the considerable scatter in drift bottle recovery sites suggests that the convergent pattern may not occur at any instant of time, but may exist only as an annual or a multi-annual net motion. Leipper (1954) noted that a surface convergence such as that appearing in the ship drift data could exist only if there were subsurface return flow. Recent drift bottle and bottom drifter studies conducted by the U. S. G. S. in Corpus Christi (Hunter *et al.* 1974) have indeed suggested that when surface motion has an onshore component, bottom flow tends to be directed offshore, and vice versa. Furthermore, Hunter *et al.*, postulate the existence of a convergence of bottom water from bottom drifter returns. Such a pattern is often displaced longshore a considerable distance from the surface convergence.

While the existence or characteristics of a convergent pattern along the Texas continental shelf has not been satisfactorily resolved, previous work has established the presence of considerable seasonable variability in the net direction of the longshore current. Watson and Behrens (1970) have used drift bottles to document a northerly drift in summer and an alternating drift in winter, due in part to periodic frontal passages. The Hydrographic Office charts, on the other hand, reflecting longer time averages and ship drift data from further offshore, indicate currents to the west-southwest in February and currents to the north in July.

Few studies have been conducted in the northwestern Gulf to investigate current variations occurring over the shorter time scales. The characteristics of tidal and inertial motions are largely unknown along the inner continental shelf in this region. Kimsey and Temple (1962) used a direct readout current meter in 27 m of water to obtain short time series, lasting on the order of a day. While it is impossible to identify the patterns as reflecting the steady current or as an anomalous perturbation on the steady flow, the considerable variation in speed and direction from one observation to the next suggests that the instantaneous current may be poorly represented by the time-integrated data provided by the ship drift or drift bottle techniques.

This study involves sub-surface current data collected during a late winter and a midsummer period in 1973. In each case, half-hourly observations over an approximately five-week period are used to investigate both short-period and seasonal variability. Simultaneously collected wind data are used to qualitatively relate surface windstress with sub-surface currents.

DATA

Half-hourly current data were obtained using an Environmental Devices Corporation Type 105 recording current meter, positioned at the 14 m level on a taut-line mooring in 18 m of water, approximately 10.8 km off Port Aransas, Texas (see Figure 1). Current speeds and directions are time-integrated over the half-hour sampling period, thus minimizing the problem of aliasing. The time integration technique involves determining the midpoint of the recorded range in current direction, and the number of turns of a ducted impeller during each half hour. Data were recorded on frames of 16 mm film. Digitization was performed by the Environmental Devices Corporation.

The recorded speed has an accuracy of ±5.9 cm/sec (0.11 kt) and a resolution of 2.6 cm/sec (0.05 kt) according to the manufacturer; the directional resolution and accuracy are ±1% at speeds above 2.6 cm/sec.

The first sampling period was a 35-day, 23-hour period from 5 February to 13 March, 1973. The second time series included a 37-day, 22-hour interval from 13 July to 20 August, 1973.

Wind data were collected at 3-hourly intervals at the U. S. Coast Guard Station at Port Aransas, just under two kilometers from the coast. The anemometer height is approximately 20 m above the ground, and 22 m above sea level.

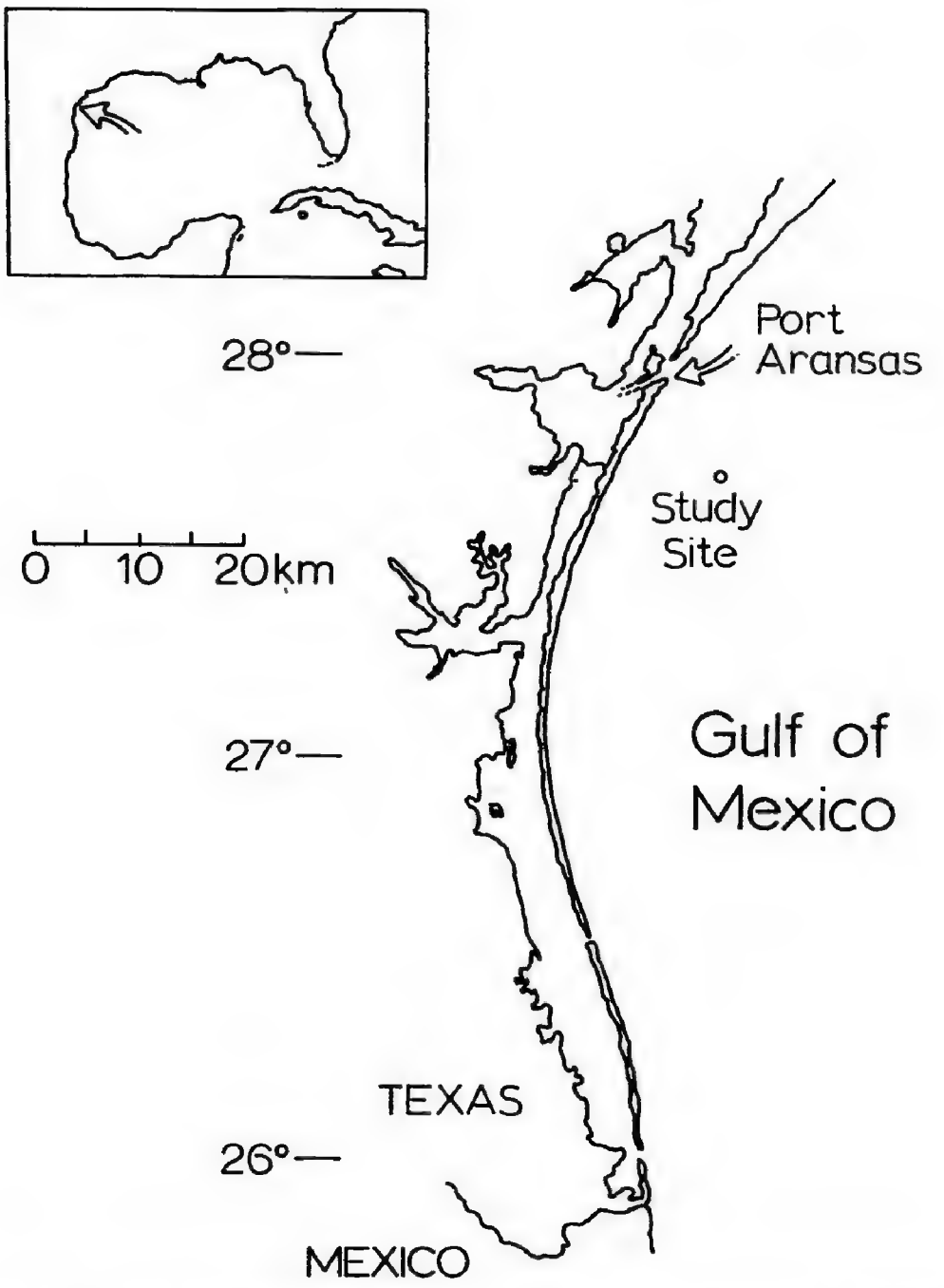

FIG. 1. Study site off Port Aransas in the northwestern Gulf of Mexico.

METHODS AND ANALYSIS

Histograms of current speed and direction were constructed using speed intervals of 3 cm/sec and directional intervals of 10°.

Energy density spectra were obtained using a computer program developed by Fee (1969). The linear trend is removed from the data prior to computing the energy density values. Phase and coherence spectra were also computed. Both time series were decomposed into the longshore (033–213°) and cross-shelf components of the current.

Current vectors were plotted in head-to-tail fashion to obtain the standard vector displacement diagram. Wind vectors were also used to construct vector displacement diagrams, after first converting wind vectors to windstress vectors, using the expression

$$\vec{\tau} = \rho\, C_z\, \vec{V}^2$$

(Roll 1965), where $\vec{\tau}$ is the windstress vector, ρ is the air density, C_z is the drag coefficient, and $\vec{V}$ is the wind velocity. Three-hourly wind data were obtained from the Coast Guard Station at Port Aransas. A value of 1.3×10^{-3} was chosen for the drag coefficient; a constant value of 1.23 kgm/m^3 was used for air density.

Twenty-nine day time series of longshore and cross-shelf current components were used to compute the harmonic constants of the principal tidal constituents (Dennis and Long 1971), which are required for the construction of tidal ellipses.

Perturbation analysis was used to investigate several aspects of the nearshore sub-surface motion. Following the normal procedure, half-hourly current vectors were broken into the mean longshore and cross-shelf ($\bar{u}$ and $\bar{v}$, respectively) and perturbation (u' and v') quantities. The coordinate axes were rotated in such a way that the x-axis passed through the ends of the vector displacement diagram. Thus $\bar{v}$, the net motion along the y-axis, equals zero and $v = v'$. In the winter data, $\bar{u}$, along the x-axis, is directed toward 251°; in the summer data, $\bar{u}$ is directed toward 229°.

Using the mean and perturbation quantities it is an easy matter to compute the kinetic energy associated with the mean flow (with $\bar{v} = 0$):

$$\text{K.E. (mean)} = \tfrac{1}{2}\,\rho(\bar{u})^2,$$

where ρ is the density of the water, and the kinetic energy associated with the turbulent motions:

$$\text{K.E. (turbulent)} = \tfrac{1}{2}\,\rho\,(\overline{u'u'} + \overline{v'v'}).$$

Finally, longshore and cross-shelf current components were numerically filtered (Groves 1955) to remove tidal period motions in the nearshore current. The local inertial period of approximately 25.8 hours corresponds closely with the period of 0_1 tidal constituent. Thus, inertial motions were also removed by the filtering process. The "D_{39}" filter described by Groves was used in this study. This filter is of the general form

$$Y(t) = \sum_{i=-n}^{n} w_i\, y(t-i), \text{ with } w_i = w_{-i},$$

where w_i are the filter weights, and y and Y are the raw and filtered current speeds, respectively.

RESULTS

The late winter current data show a marked constraining effect of the coast. The progressive vector diagram constructed from these sub-surface currents (Figure 2) indicates a slightly meandering current toward the west-southwest (251°). There is a generally continuous flow, with the exception of one brief episode between 24 and 26 February, when a small cyclonic loop appears in the pattern.

The direction histogram (Figure 3) shows a strong concentration of currents between 220° and 270°, with a maximum between 240° and 250°. This indicates a slight onshore component. The local orientation of the coastline is approximately 033°–213°, and the orientation of the 18 m isobath is 035°–215°.

Figure 4 shows the frequency of current speeds from the winter time series. Current speeds lie generally between 12 and 30 cm/sec, averaging approximately 21.5 cm/sec (0.42 knot). Currents of up to 66 cm/sec were recorded during this 36-day interval. While there is a marked constriction in direction by the coast, the longshore current does exhibit a broadly skewed pattern in the distribution of speeds.

The relative energy density spectra computed from both the longshore and cross-shelf components of the late winter data (Figure 5) show a fairly smooth decrease in energy levels with decreasing period. No significant increase in energy density levels is indicated at the diurnal or semi-diurnal tidal periods. Nor is there a peak at the local inertial period of 25.8 hours. There is a distinct rise in energy levels in the longshore component spectrum at a period of just

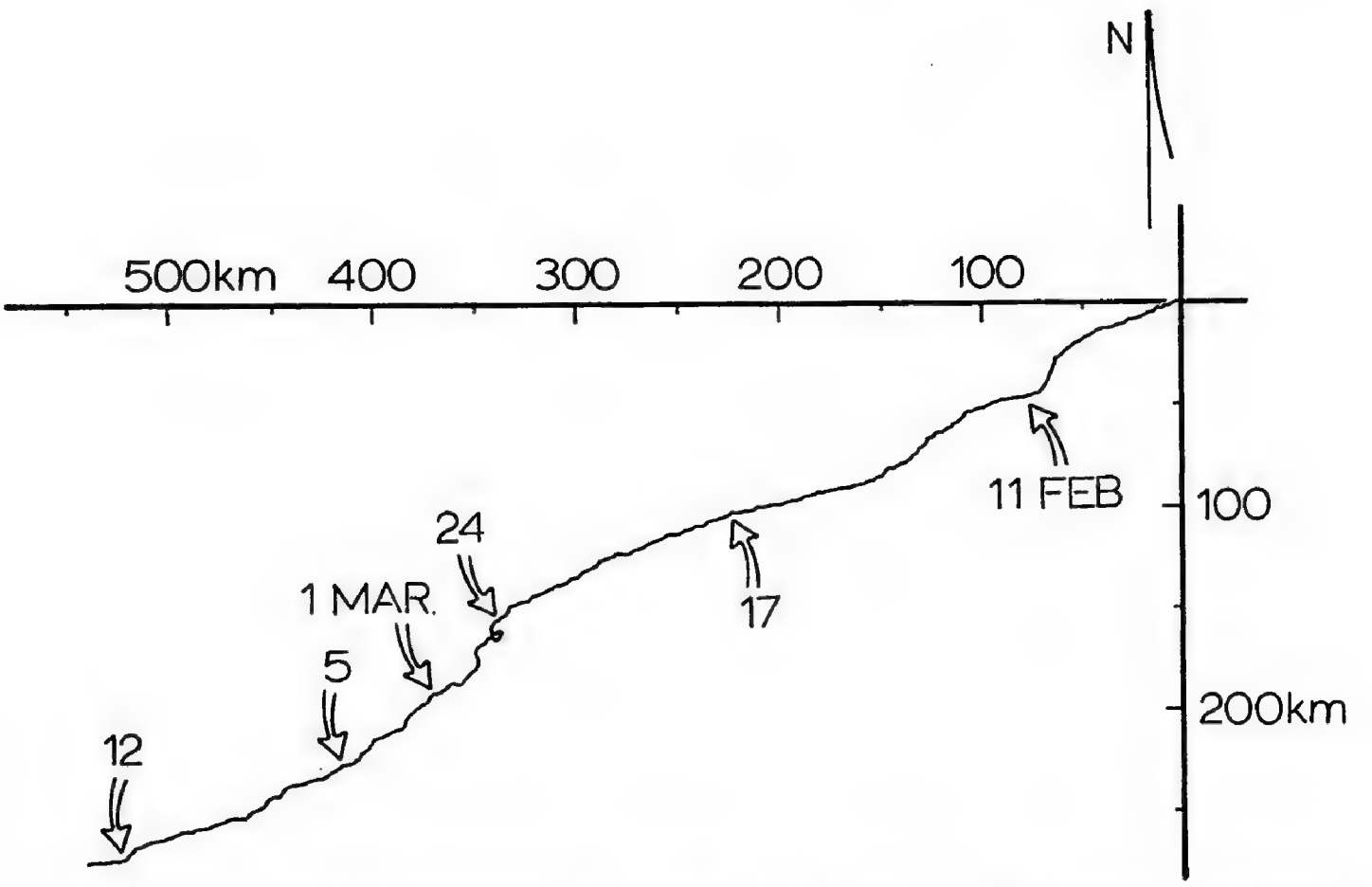

FIG. 2. Vector displacement diagram, 5 February to 13 March, 1973. 14 m level. See Figure 1 for study site location. Arrows point to displacement at 1500 CST.

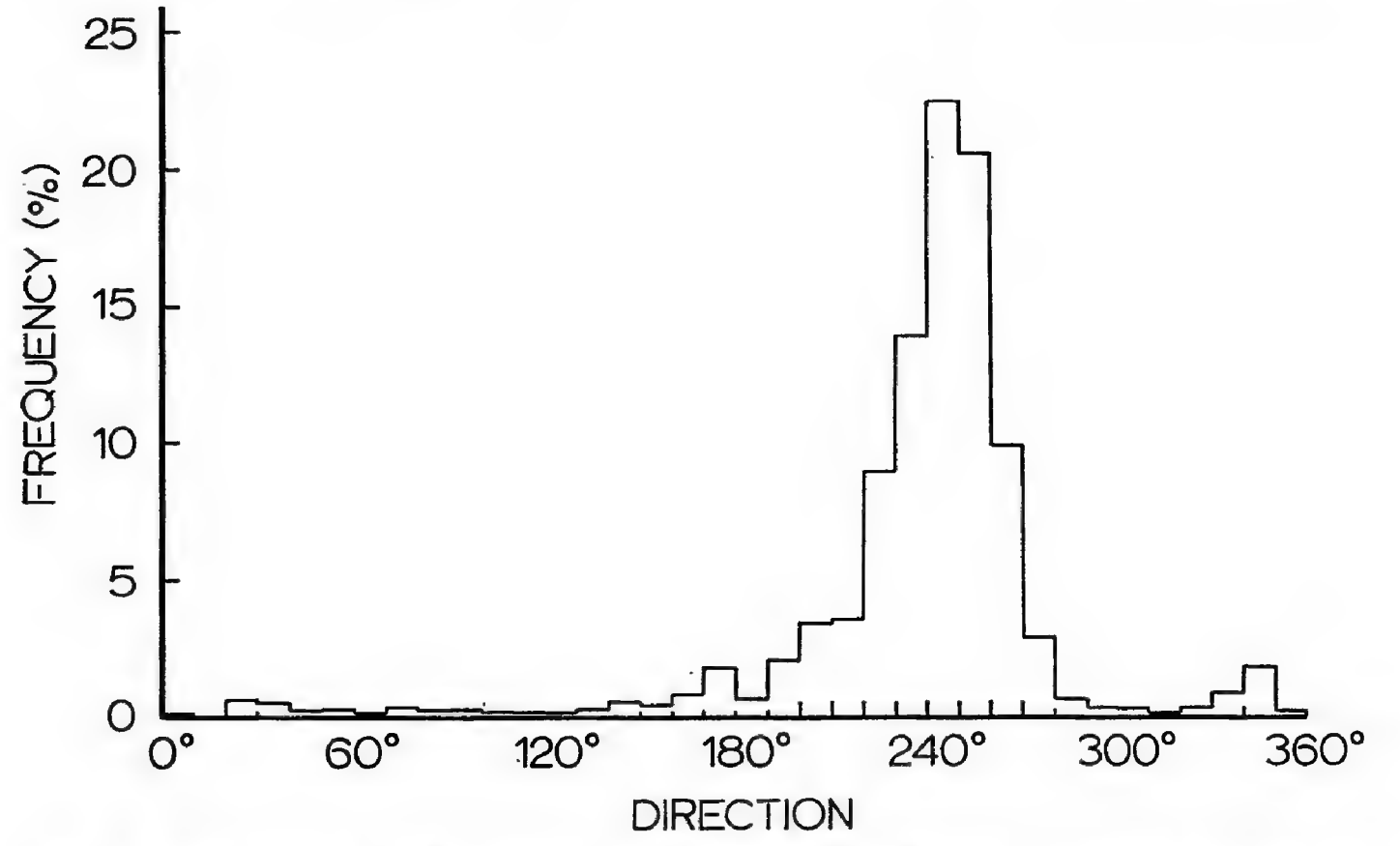

FIG. 3. Histogram of current direction (10° intervals) vs. percent, 5 February to 13 March, 1973. 14 m level.

under 18 hours, though there is no apparent physical basis for this. Variations in energy levels become somewhat irregular at periods below approximately five

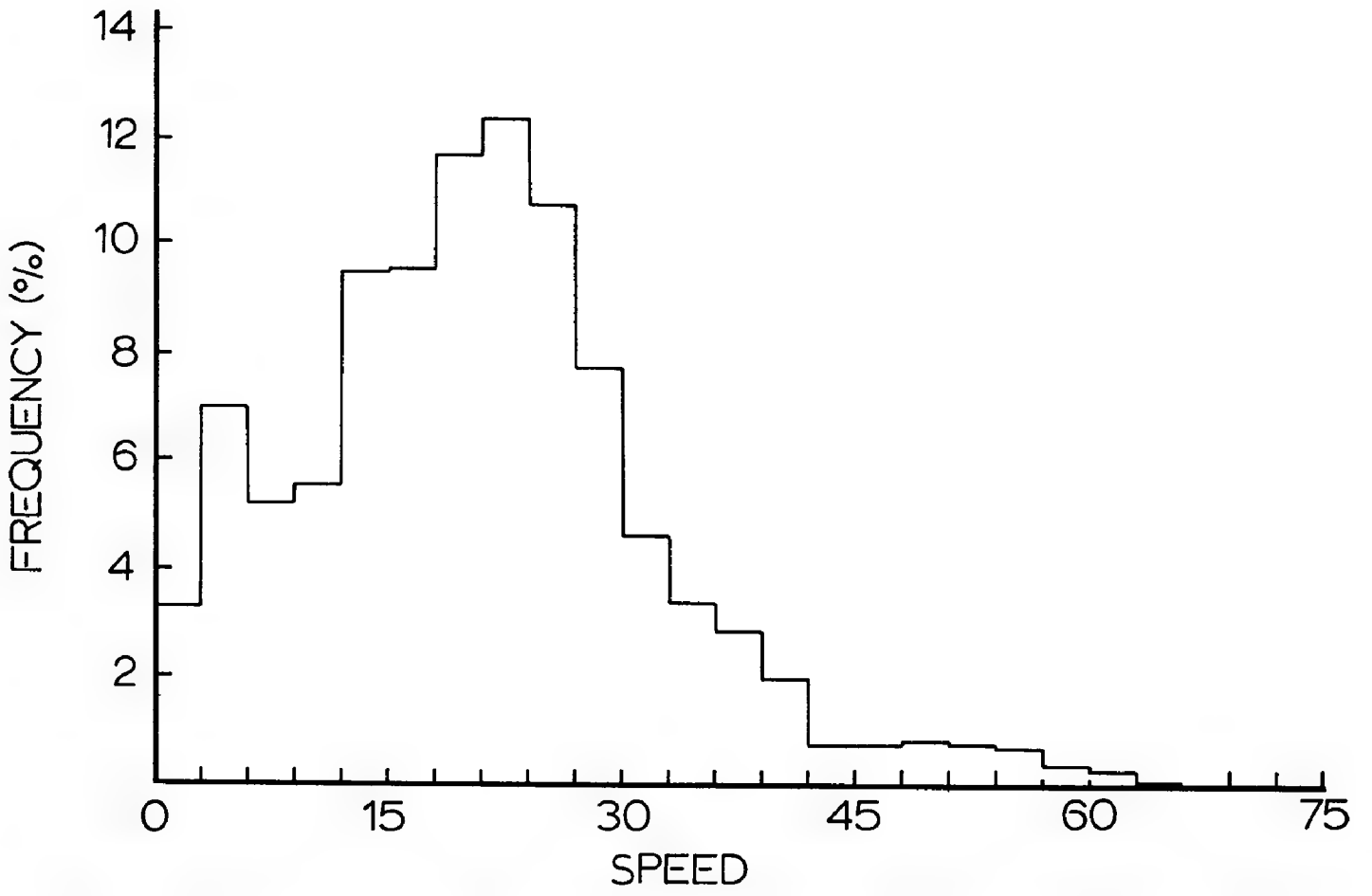

FIG. 4. Histogram of current speed (3 cm/sec intervals) vs. percent, 5 February to 13 March, 1973. 14 m level.

hours with no statistically significant peaks. Energy density values at periods of between one and two hours have not been plotted. The coherence spectrum from longshore and cross-shelf current components (Figure 6) is characterized by low values except at the longest periods. Coherence-squared values at diurnal and semi-diurnal tidal periodicities are both about 0.13.

The progressive vectors computed from the July-August data (Figure 7) indicate a significantly different pattern, with longshore currents reversing in direction at intervals of between one and two weeks. Relatively short period, tidal motions are superimposed onto the general drift. At times, the longshore current weakens to the extent that tidal oscillations become complete rotations. The progressive vectors suggest that well developed, tidal period reversals in direction can displace water parcels distances on the order of 3–5 kilometers before returning to the approximate starting point.

The direction histogram of the summer data (Figure 8) shows a twin-peaked distribution. Longshore currents have a preference for directions between 160°–240° and between 320°–050°. Thus, the northerly longshore motion has an onshore component at the 14 m level; the southerly current moves slightly offshore. The net transport in the summer data is approximately to the southwest (229°).

Figure 9 shows the histogram of summer current speeds. The pattern is similar to that found in the winter currents, though the skewed distribution is displaced toward slower speeds. Currents vary generally between 3 and 15 cm/sec, with

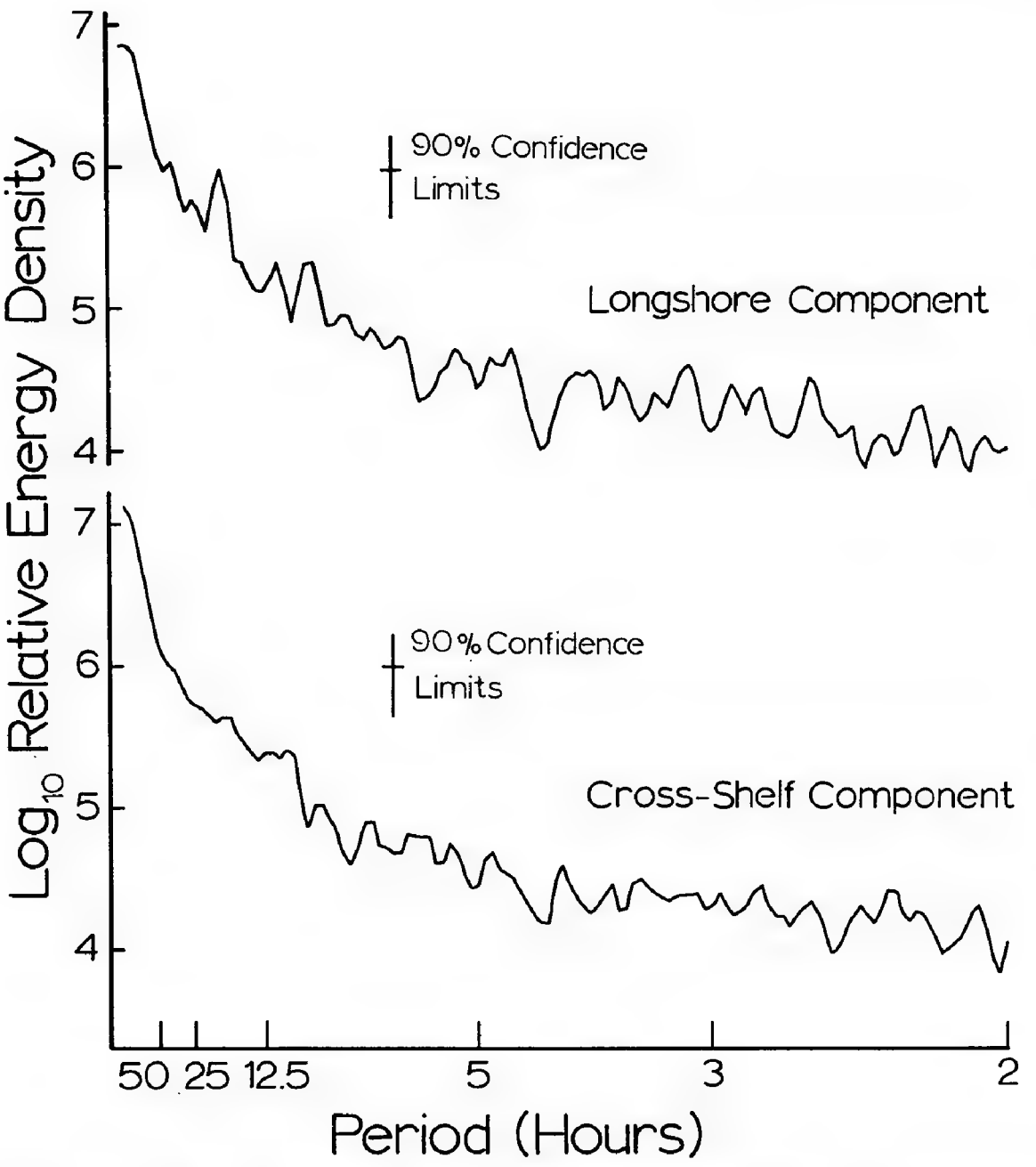

FIG. 5. Relative energy density spectra of longshore and cross-shelf current components. 14 m level. 5 February to 13 March, 1973. Computed with 250 lags. Energy density values at periods between one and two hours not plotted.

an average of 10.5 cm/sec. There is a significant difference, however, between the average current speed and the resultant current speed. The cancellation effect of an alternating longshore current reduces the resultant speed to only 2.5 cm/sec, suggesting little net transport during this time.

The relative energy density spectrum (Figure 10) indicates substantially less long-period meandering in the summer currents than in the winter currents. There is a pronounced peak at the 24-hour period. Tidal motions clearly dominate both the longshore and cross-shelf motions over this time interval. The spectral peaks at periods of less than about 10 hours are probably not significant.

The coherence spectrum of the summer component data (Figure 11) shows high values at the diurnal tidal periodicities, reaching a maximum of over 0.9 at a period of 25 hours. Again, high coherence-squared values are associated with the longest period motions. Values at periods shorter than about twenty hours are probably not significant.

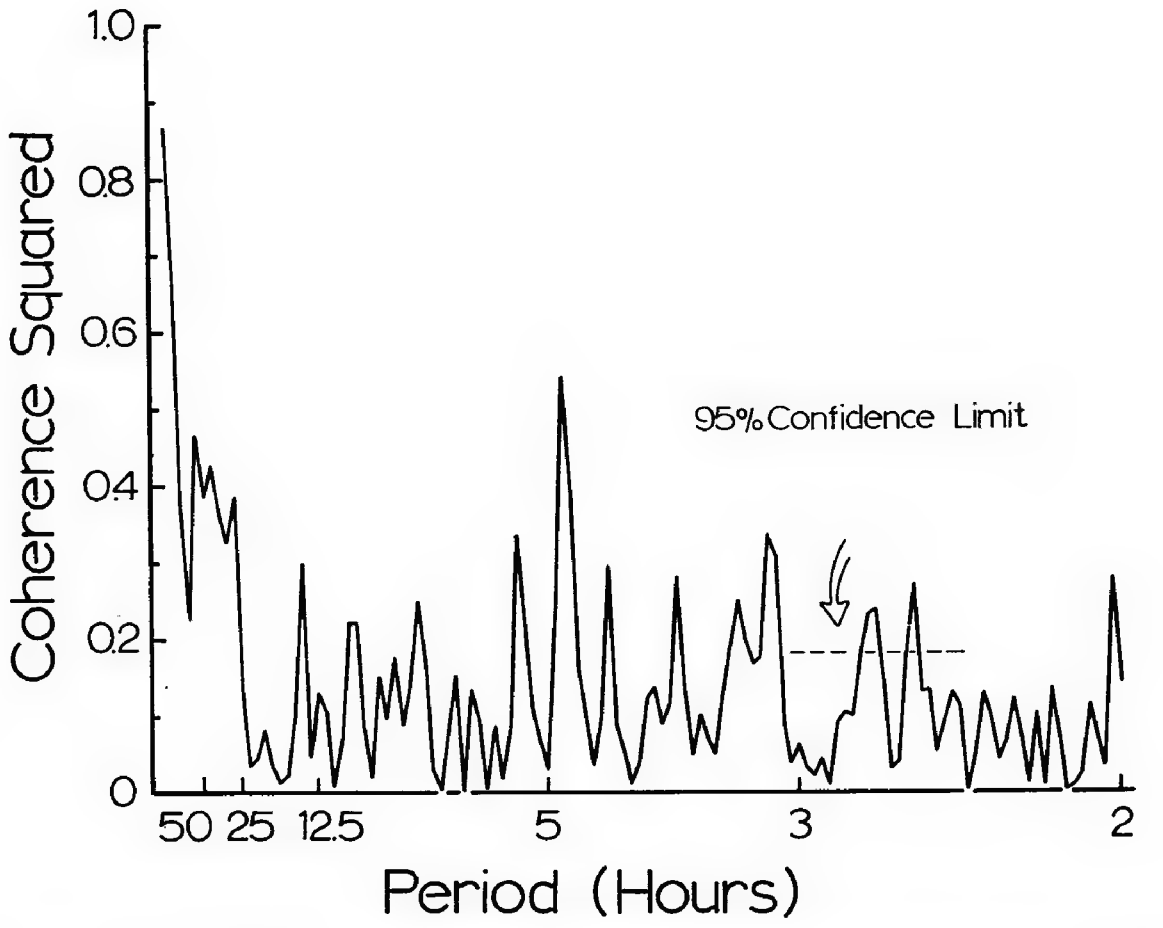

FIG. 6. Coherence spectrum for longshore and cross-shelf current components. 14 m level. 5 February to 13 March, 1973.

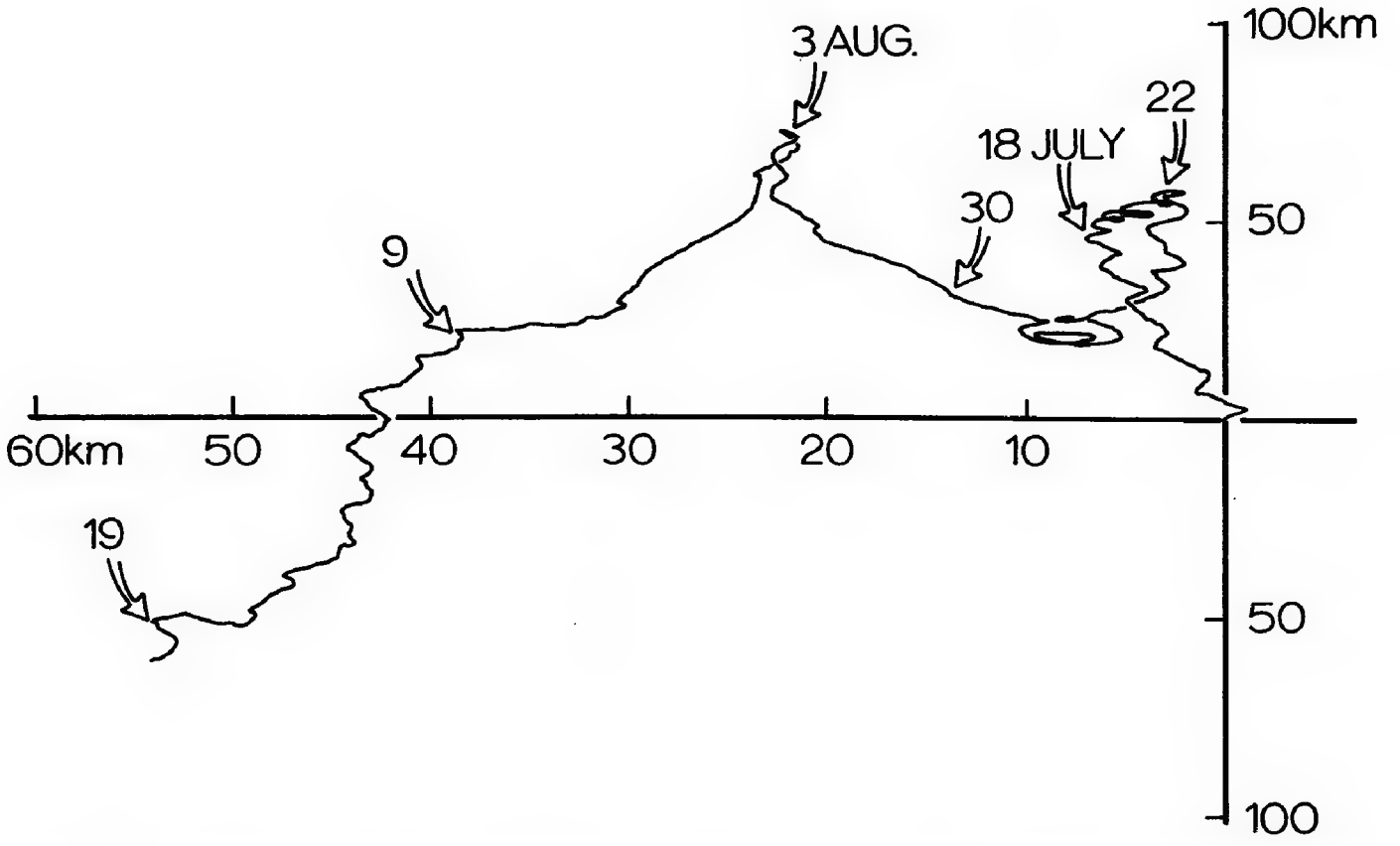

FIG. 7. Vector displacement diagram, 13 July to 20 August, 1973. 14 m level. See Figure 1 for study site location. Arrows point to displacement at 1700 CST.

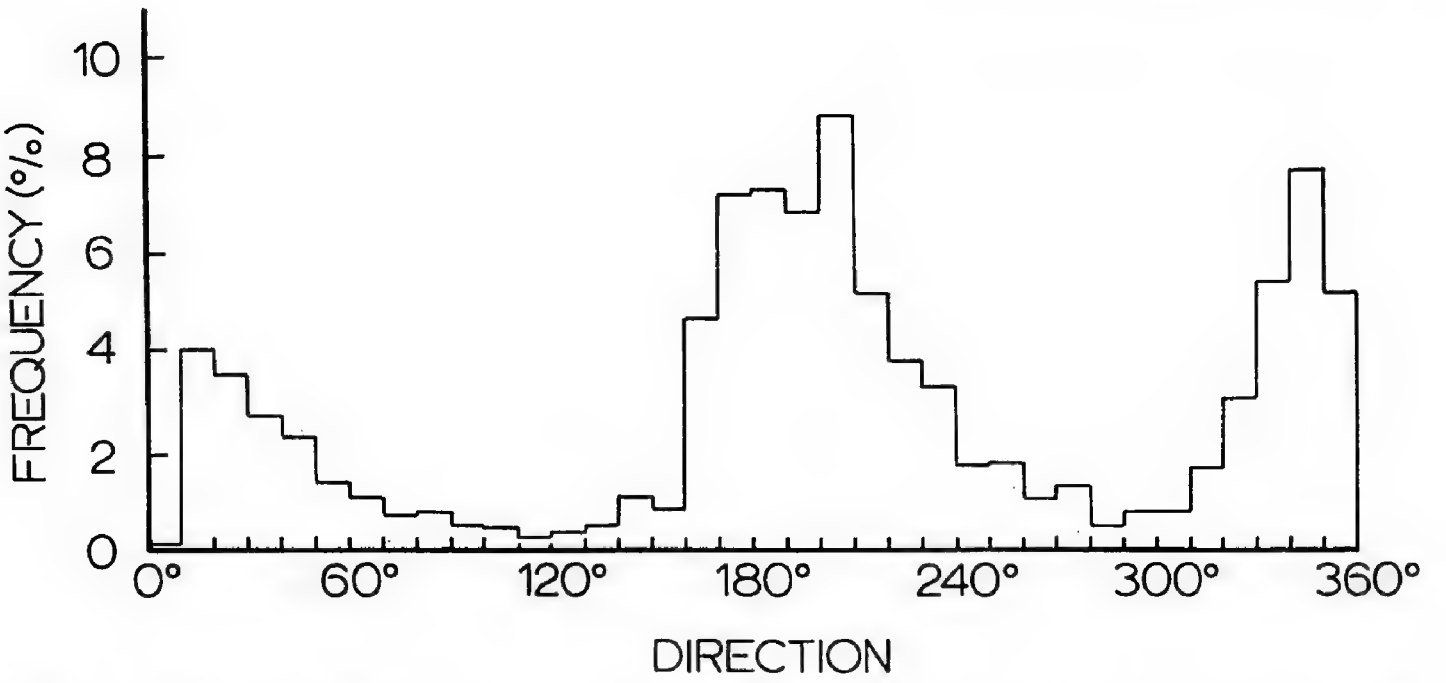

FIG. 8. Histogram of current direction (10° intervals) vs. percent, 13 July to 20 August, 1973. 14 m level.

Windstress vector displacements between 5 February and 13 March (Figure 12) show a net stress to the southwest (215°). Significant departures from this direction, however, occur both early and late in the sampling period. Light southeasterly winds are indicated between 5 and 8 February, and again between 12 and 14 February. From 28 February through 13 March winds are light and somewhat variable, but generally from the east-southeast. Strongest winds are north-northwesterly on 8 and 9 February, and north-northeasterly between 14

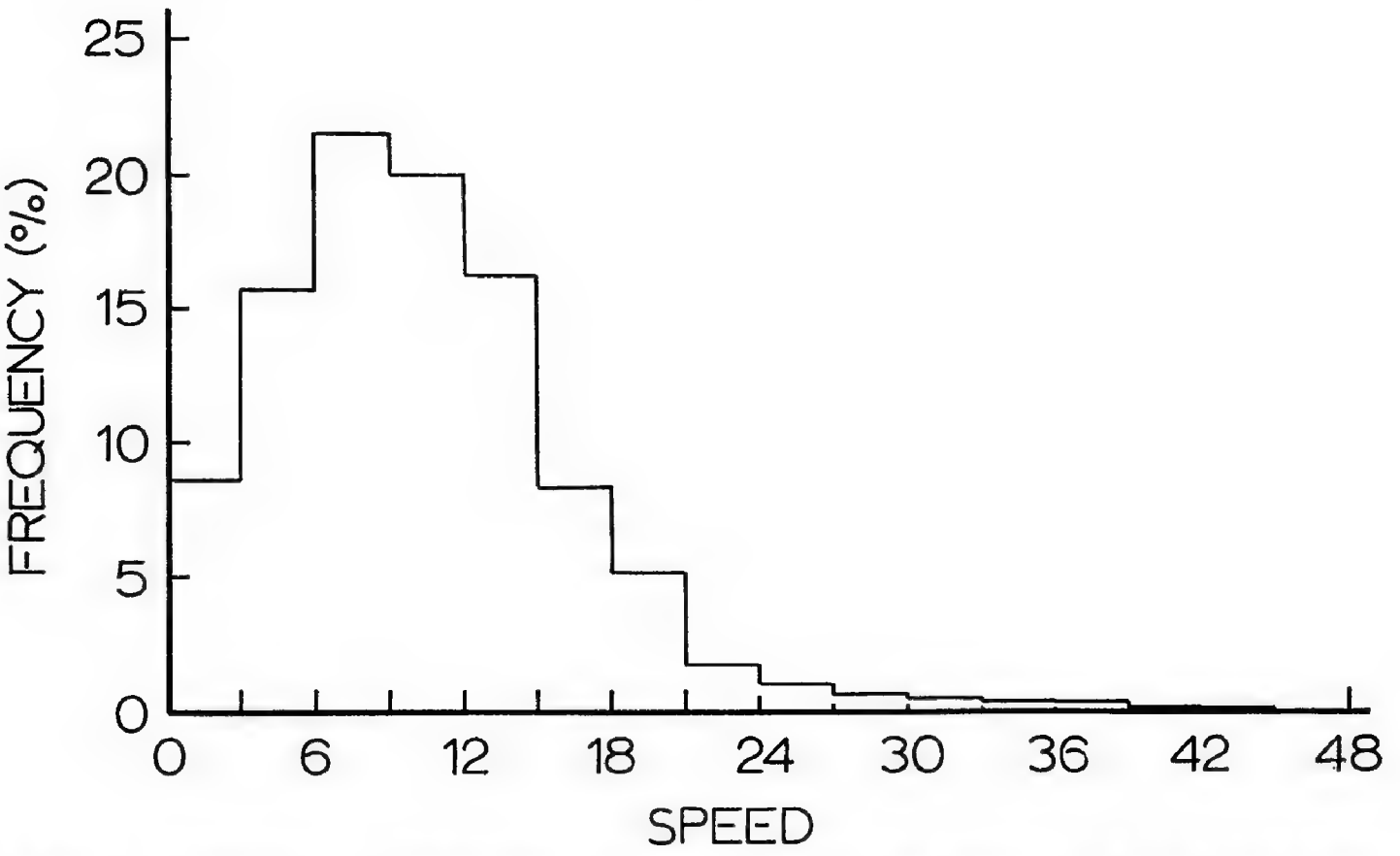

FIG. 9. Histogram of current speed (3 cm/sec intervals) vs. percent, 13 July to 20 August, 1973. 14 m level.

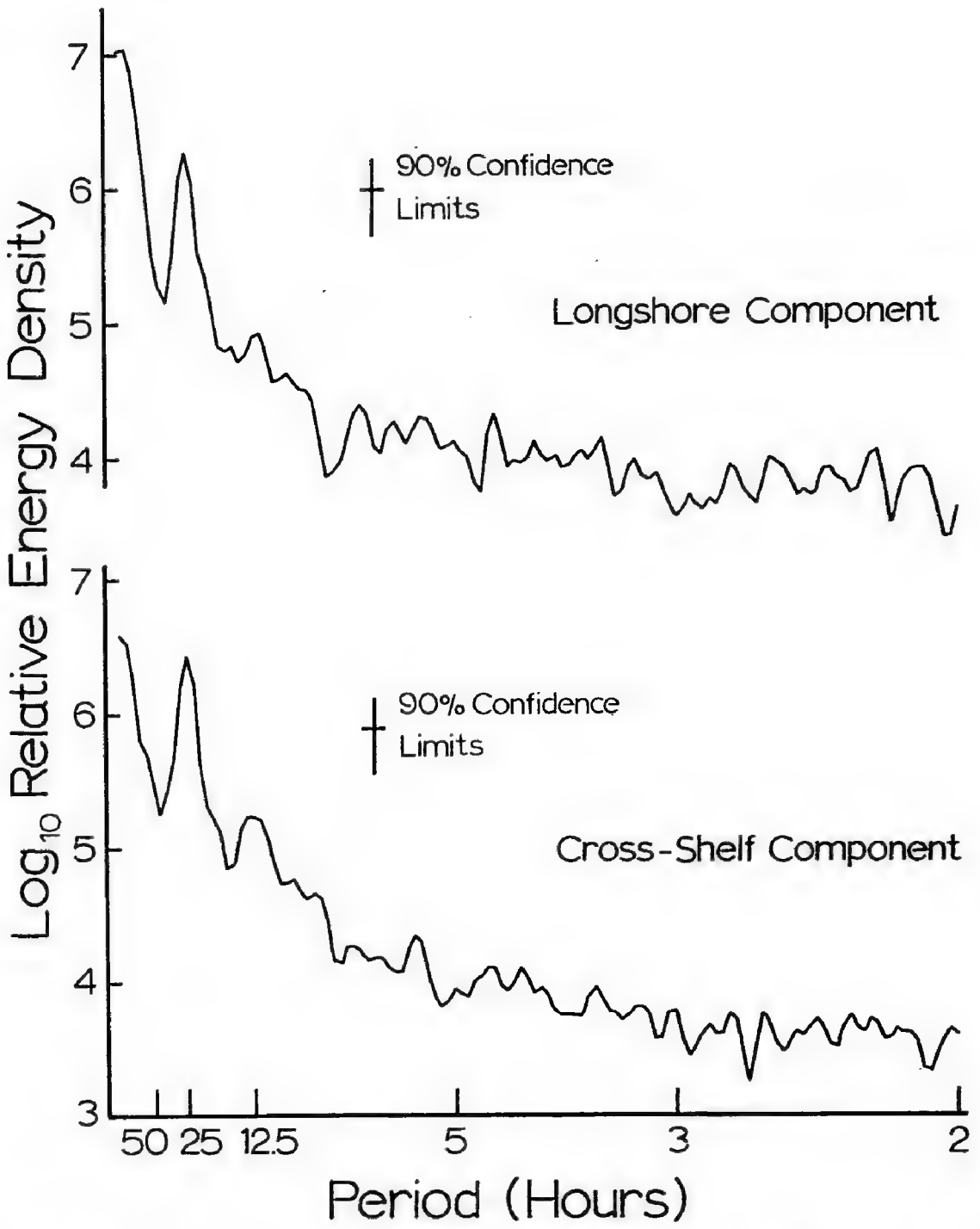

FIG. 10. Relative energy density spectra of longshore and cross-shelf current components. 14 m level. 13 July to 20 August, 1973. Computed with 250 lags. Energy density values at periods between one and two hours not plotted.

and 24 February. Diurnal displacements may be approximated by interpolating between the labelled two-day intervals.

The windstress vector displacement between 12 July and 10 August (Figure 13) indicates a net stress force to the northwest, nearly perpendicular to the coast. The record is broken by approximately two days of no data, then resumes with a week of variable but generally easterly winds. Strongest winds are southeasterly, occurring on 29 and 30 July.

Numerical filtering of the longshore and cross-shelf current components indicates the extent to which tidal and inertial motions occur in the data. The variance of the current components was computed before and after the data were filtered. Results are shown in Table 1.

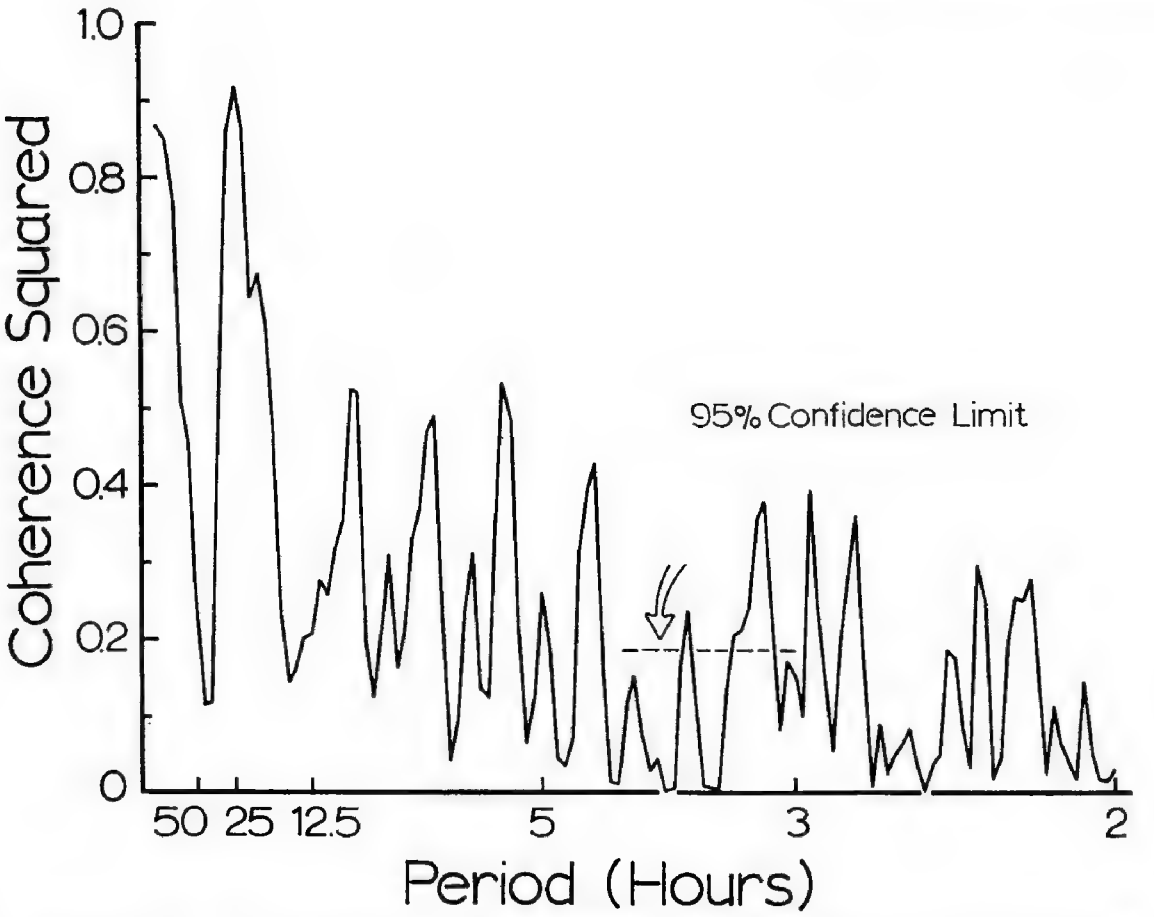

FIG. 11. Coherence spectrum for longshore and cross-shelf current components. 14 m level. 13 July to 20 August, 1973.

In the winter data, over 80% of the variance remained following the removal of tidal and inertial period motions. In the summer data, 83% of the longshore variance remained, while cross-shelf motions were diminished to 56% of their former value. This suggests that the alternating longshore currents recorded in the summer contain tidal and inertial motions largely in the form of cross-shelf meanders.

Twenty-nine day segments of the longshore and cross-shelf current components were used to compute the harmonic constants of the principal tidal constituents in the current record. Amplitudes and phase angles are given in Table 2.

Tidal ellipses have not been constructed due to the high degree of variability between the corresponding harmonic constants computed from the winter and summer data. For example, K_1 amplitudes increase by nearly an order of magnitude from the winter to the summer data, and the longshore and cross-shelf component phase angles suggest that the K_1 constituent rotates anticyclonically in winter but cyclonically in summer. There is a similar indicated reversal in the rotation of the O_1 tidal constituent current. All computed tidal constituent amplitudes are well below the accuracy of the current meter. The statistical significance of the amplitudes has not been computed, but their validity is doubtful.

One of the greatest differences between the winter and summer data appears in the distribution of kinetic energy between the mean and turbulent motion. In the winter data, the kinetic energy in the quasi-steady longshore current exceeds that of the turbulent motions by nearly a factor of two (see Table 3), while in the summer data the kinetic energy of the turbulent motion is nearly two orders of magnitude greater than that associated with the mean flow.

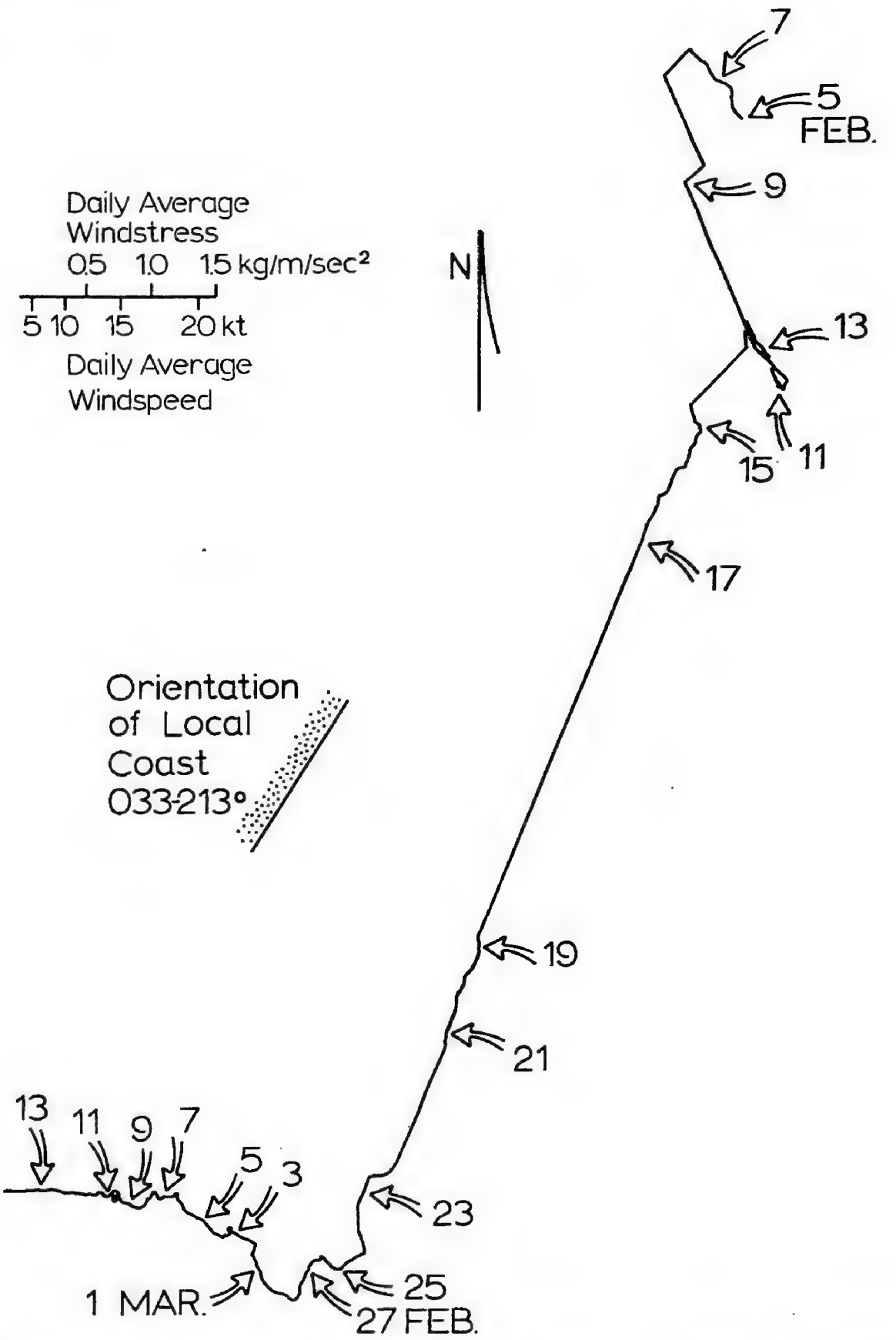

FIG. 12. Vector displacement diagram of windstress vectors, 5 February to 13 March, 1973. Wind data were collected at the Coast Guard Station at Port Aransas (see Figure 1). Arrows point to displacement at 1700 CST.

DISCUSSION

Seasonal variability in circulation patterns is to be expected in view of annual cycles in heating and surface windstress. The apparent decrease in tidal period motions in the winter data (Table 2), coupled with the well-defined diurnal peak in the energy density spectra of the summer data, is surprising in view

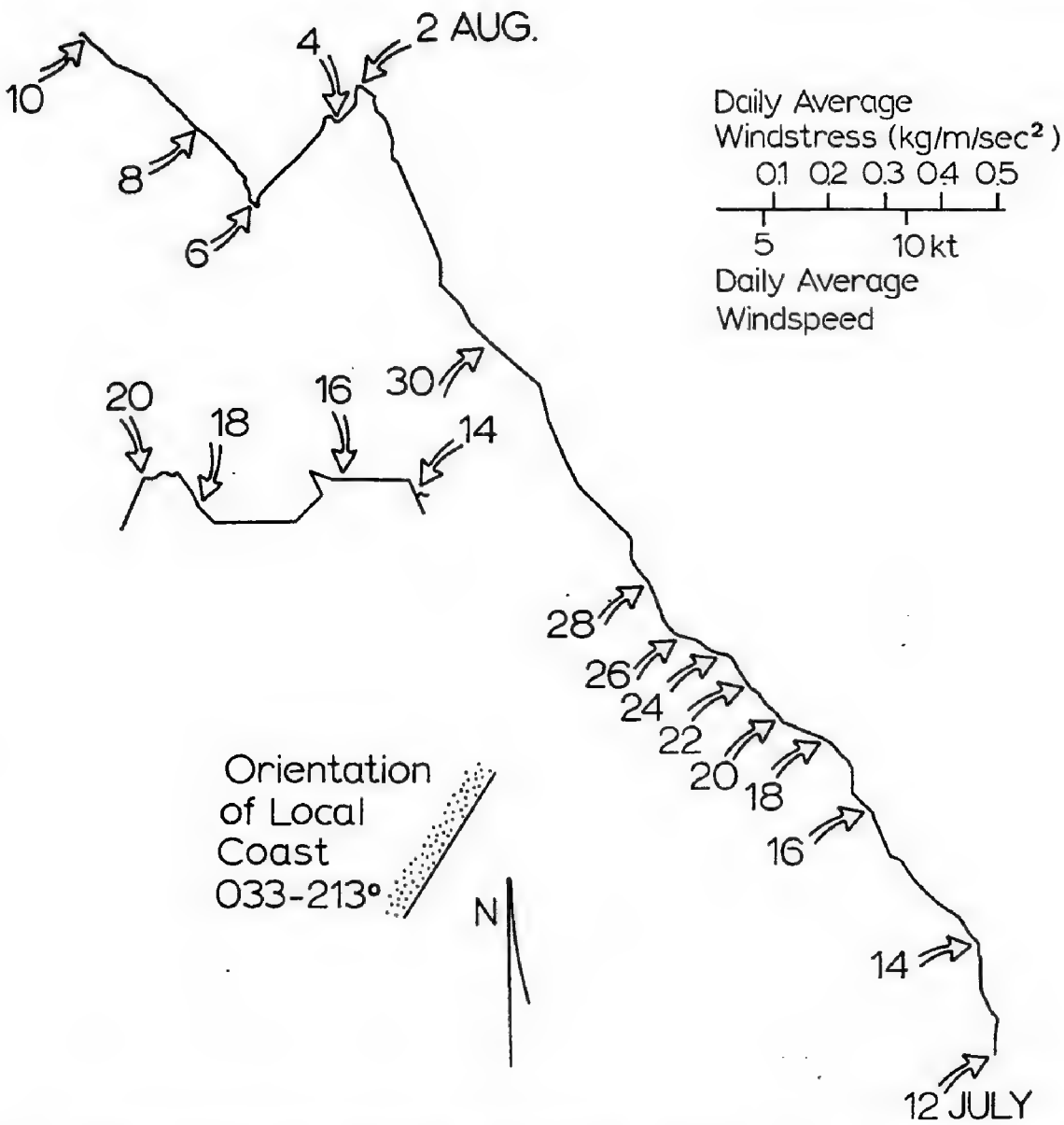

FIG. 13. Vector displacement diagram of windstress vectors, 12 July to 10 August and 13 to 20 August, 1973. The origin of the final eight days of data has been arbitrarily displaced. Wind data were collected at the Coast Guard Station at Port Aransas (see Figure 1). Arrows point to displacement at 1700 CST.

TABLE 1

Variance of Unfiltered and Filtered Current Component Data

	Unfiltered	Filtered	Filtered/Unfiltered
A. Winter Time Series			
1. Longshore Components	112.7 cm^2/sec^2	93.7 cm^2/sec^2	0.83
2. Cross-shelf Components	107.9 cm^2/sec^2	87.9 cm^2/sec^2	0.81
B. Summer Time Series			
1. Longshore Components	70.6 cm^2/sec^2	58.5 cm^2/sec^2	0.83
2. Cross-shelf Components	29.9 cm^2/sec^2	16.7 cm^2/sec^2	0.56

of the fact that there is no corresponding annual variation in the diurnal and semi-diurnal tidal forces. A possible explanation is that tidal-period variations in the longshore flow at the study site may be largely a result of the influence of water flooding into or ebbing from the channel at Port Aransas (see Figure 1). In the winter, the strong longshore flow can provide flood water from the up-

TABLE 2

Harmonic Constants of Principal Tidal Constituents. Amplitudes, η, in cm/sec; local phase angles, κ, in degrees

		K_1	O_1	M_2	S_2
A. Winter Time Series (29 days, starting 5 February, 1973)					
1. Longshore Components	η	0.40	1.42	0.58	0.50
	κ	159.3	193.0	49.0	84.0
2. Cross-shelf Components	η	0.62	0.69	0.94	0.79
	κ	49.8	268.1	51.9	127.6
B. Summer Time Series (29 days, starting 13 July, 1973)					
1. Longshore Components	η	3.06	1.86	0.44	0.70
	κ	29.5	44.3	96.9	204.8
2. Cross-shelf Components	η	4.13	1.48	0.64	0.37
	κ	126.1	142.1	185.7	254.4

TABLE 3

Distribution of Kinetic Energy in Mean and Turbulent Motions

	Mean Motion	Turbulent Motion	Mean/Turbulent
A. Winter Time Series	195.6 gm/cm/sec^2	107.5 gm/cm/sec^2	1.82
B. Summer Time Series	3.2 gm/cm/sec^2	76.4 gm/cm/sec^2	0.042

stream side, then hold the ebbed water too close to the coast for its effects to be felt at the study site, slightly downstream of the channel. With characteristically weaker longshore currents in summer, the tidal ebbing and flooding through the channel is apparently capable of effecting a cross-shelf deflection in the longshore motion.

The wind and current data presented here support the idea of a strong interdependence between the circulation along the inner Texas continental shelf and the overlying wind field. A comparison of the windstress progressive vector diagrams (Figures 12 and 13) with the sub-surface current progressive vector diagrams (Figures 2 and 7, respectively) suggests that many of the long-period variations in the current speed and direction can be explained by the local winds. The alternating summer current agrees quite well with the alternating longshore component of the generally onshore surface winds. The shift in the longshore current on 3 August from a northwesterly to a southwesterly direction corresponds closely in time with a change from north-northwesterly to southwesterly directed windstress vectors. In the winter data, the longshore current to the west-southwest is clearly in response to the west-southwesterly directed longshore component of the surface winds. A sudden deceleration in current speed corresponds with the transition from strong northeasterly winds to light and variable winds on about 24 February. The three episodes of northwesterly or west-northwesterly windstress, however, are not reflected in the sub-surface current data.

A high correlation between sub-surface currents and local winds should not

necessarily be expected in view of the spatial variability in surface winds. Franceschini (1953), in computing mean monthly windstress vectors, demonstrates considerable variability in both the magnitude and the direction of the windstress vectors in the northwestern Gulf of Mexico. Local currents should be thought of as part of a larger scale circulation pattern. Local winds may have a direct effect in modifying the local circulation, but the currents measured off Port Aransas may be substantially influenced by a spatially integrated windstress force covering much of the northwest corner of the Gulf of Mexico.

Additional wind data and especially circulation data are required to investigate the existence or characteristics of a convergence along Padre Island, as has been suggested in previous studies. The winter and summer data presented here are certainly not adequate for defining a net annual convergence, but the subsurface current data are consistent with a net annual convergent pattern centered south of the study site. The strong longshore flow to the southwest in winter, and alternating flow in the summer data suggest a net annual transport of water to the south along the inner shelf off Port Aransas. If a strong northeasterly flow in summer and alternating currents in winter were recorded further down the coast well south of latitude 27°, the net annual convergence could be confirmed.

The slow, anticyclonic turning of the sub-surface current vectors observed during the first two weeks of the summer time series indicates that the nearshore circulation is more complex than a simple alternation of a longshore current. The period between 18 and 22 July is one of weak winds moving nearly directly onshore, but with slow sub-surface currents moving nearly directly offshore (neglecting the tidal period oscillations). Hunter, *et al.*, have documented a return flow using drift bottles and bottom drifters, and the current meter may have been recording such a return flow at this time. Drogue studies conducted off the Gulf coast of Florida (Stephen P. Murray, personal communication) indicate significant directional shear through the water column and a strong dependence on vertical density structure. No hydrographic data were taken as part of the present study. The persistent onshore component of the sub-surface current occurring over much of both the summer and winter study periods may reflect directional shear in an Ekman layer, or some other form of dynamic balance in the nearshore water column. Additional current profile data would be required to investigate this aspect of the nearshore circulation.

The tidal period and longer variations noted in the vector displacement diagram of the summer data point out the danger associated with sampling over too short a time interval. Clearly, a single current measurement would be inadequate to determine the local drift when tidal forces are strong enough to temporarily reverse the flow. Similarly, measurements made over even several days would be insufficient to detect the alternating nature of a current responsive to the longshore component of the wind. The computed seasonal variations in the amplitude and phase angles of the principal tidal constituents indicate that even studies lasting the 29 days required to compute the harmonic constants may in fact yield highly misleading results for this component of the total circulation.

CONCLUSIONS

The winter and summer current data presented here indicate that the circulation of the inner Texas continental shelf is primarily wind-driven, though with often substantial tidal motions. A qualitative comparison with wind data suggests that the correlation between currents and surface windstress is often poor when considering the more transient features. Perturbation analysis indicates that there is a significant seasonal variation in the distribution of kinetic energy between the quasi-steady and the turbulent components of the current.

Tidal period motions appear to be poorly developed, and may well exist primarily as a consequence of water moving into and out of the coastal bays through the nearby channel.

As would be expected, nearshore motion exists through a broad range of periodicities. This study is the first in this part of the Gulf of Mexico to investigate the magnitude and characteristics of the shorter period components of the circulation which have been impossible to detect using drift bottle and ship drift data.

ACKNOWLEDGMENTS

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FIDDLER CRABS IN A NONTIDAL ENVIRONMENT

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ABSTRACT

Three recently described species of fiddler crabs (genus *Uca*, family Ocypodidae) occur in nontidal habitats on Mustang Island, Texas. *Uca panacea*, the most common species, inhabits a wide variety of microhabitats, from dry-damp sand flats to wet sand-mud algal flats. *Uca virens* prefers wet mud substrates and *Uca longisignalis* is uncommon, inhabiting dry-damp sand-mud zones. The latter two species are always associated with clumps of vegetation, whereas *U. panacea* often inhabits denuded sand flats.

Uca panacea was studied in the field and in the laboratory with regards to burrowing behavior, dispersion, substrate preferences and reaction to submersion in sea water. When 50 adults were translocated from a nontidal area to a tidal area, all the crabs subsequently recovered were found in the supratidal zone.

The ecological and behavioral consequences of nontidal environments include: 1) the availability of surplus semi-permanent burrows for refuge; 2) additional display, courtship and feeding time; and 3) changes in social behavior and predator-prey relationships. These adaptations may be significant in the evolution of social behavior in fiddler crabs, but the need for more detailed comparative studies to relate ecological and behavioral patterns is noted.

INTRODUCTION

Fiddler crabs (genus *Uca*, family Ocypodidae) are common intertidal inhabitants of marshlands, salt flats, and mangrove swamps of tropical and neotropical coastlines. These semiterrestrial animals burrow into a wide variety of substrates, from coarse beach sand to fine clay-containing marsh mud (Teal 1958) and they can tolerate a relatively wide range of temperatures (Miller and Vernberg 1968), salinities (Miller and Maurer 1973) and humidity conditions (Edney 1961). In habitats where *Uca* has been studied intensively, periodic tidal inundation is usually a prominent feature, providing an environmental regulator for feeding, burrowing, courtship, color changes and locomotor activity (Barnwell 1966; Bennett, Shriner and Brown 1957; Crane 1958; Fingerman 1957).

On Mustang Island, located east of Corpus Christi in the Texas barrier island chain, nontidal populations of *Uca* were investigated over a two-year period (Powers 1975). Unlike populations of *Uca tangeri* studied by Altevogt (1959) that included adjacent intertidal and nontidal colonies, no intertidal populations of *Uca* have been found on Mustang Island. This report is a description of the habitats and some burrow-related activities of these *Uca* populations, plus a brief discussion of differences between nontidal and intertidal environments as factors in the social relationships of fiddler crabs.

DESCRIPTION OF HABITATS

Ecological surveys were conducted at four sites on Mustang Island, selected to represent the full range of habitats in which fiddler crabs were commonly encountered. Only a few of the roads and other features are shown (Fig. 1) for reference. Site IV, located at the southern end, is not shown.

Site I is an algal flat that undergoes seasonal flooding from heavy rainfall and northern wind tides during the winter, creating a broad but shallow inland pond with connections to the channel side of the island. Evaporation and drainage during the summer and fall isolate the pond and reduction proceeds until only a dry mud flat remains. The substrate ranges from mud-sand to fine mud with a high clay content. Organic content is also high, provided by frequent algal blooms and large populations of fish fry, small crabs, shrimp and other organisms. A vegetated barrier flat surrounds the algal flat. Dominant plants include *Distichlis spicata, Monathochloe littoralis, Salicornia bigloveii* and two species of *Spartina.* This is the wettest of the four sites, due to slower drainage through a less porous substrate and the site's overall low elevation.

Site II borders the Corpus Christi ship channel and consists of old spoil bank

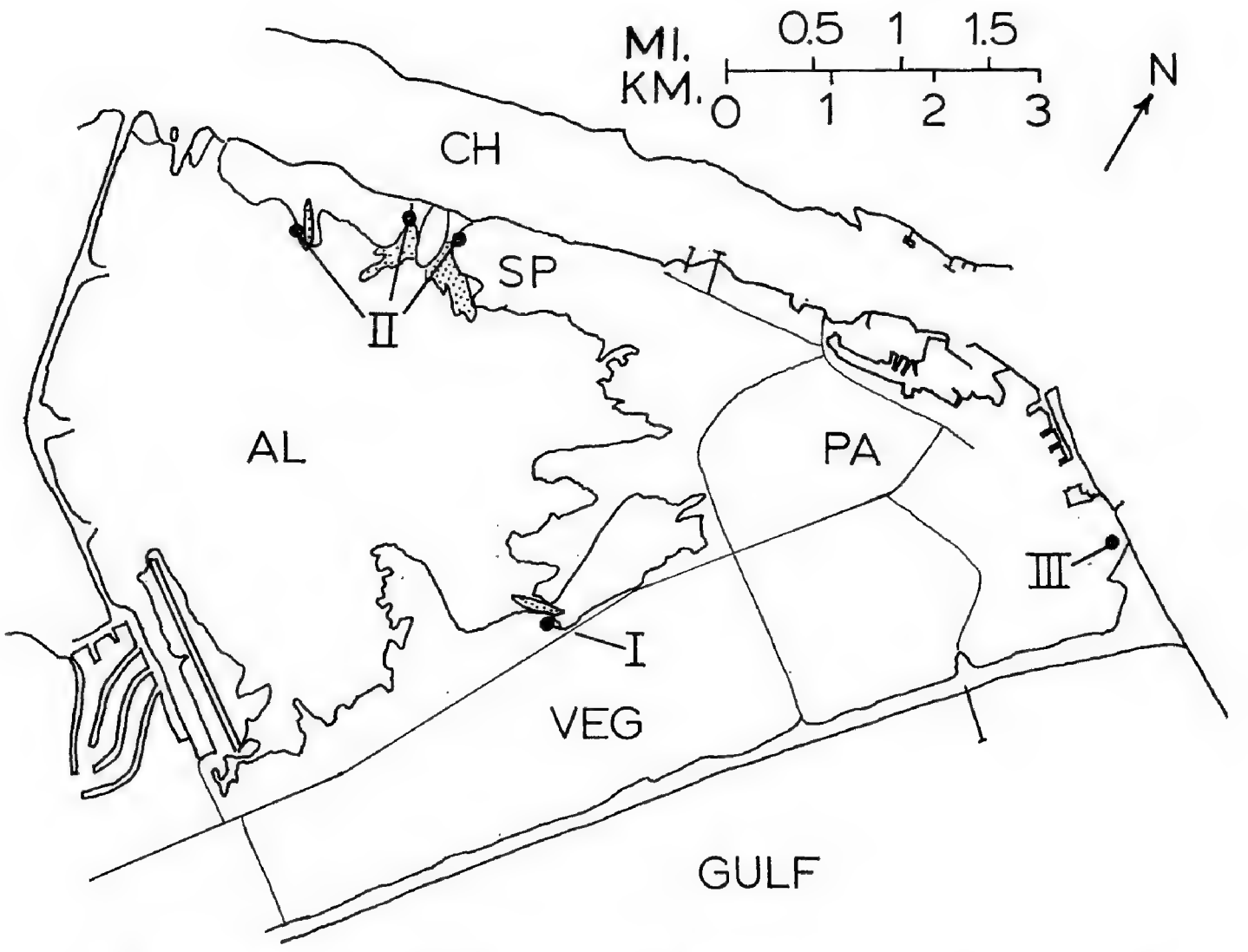

FIG. 1. Map of the northeastern end of Mustang Island. Roman numerals indicate sites I, II, and III. N is the direction of true north. AL = algal flats, CH = Corpus Christi Ship Channel, PA = Port Aransas, SP = spoil bank deposits, VEG = vegetated barrier flats. Stippled areas are salt water ponds near *Uca* sites; light lines are major roads or streets.

deposits from channel dredgings interspersed with small sand flats and semi-permanent saltwater ponds. Vegetation, mostly *Distichlis* and *Spartina*, has stabilized the spoil banks and crab burrows occur mainly at the borders between these elevated grass areas and the adjoining sand flats. The substrate is mainly sand with localized shell concentrations and it has rapid surface drainage. Clumps of *Spartina alterniflora* are present where mud is mixed with sand.

Site III lies along the South Jetty, behind the University of Texas Marine Science Institute, and it contains a vegetated barrier flat interspersed with sand-gravel and shell spoil bank deposits. *Spartina patens* and clumps of *Spartina spartina* are the dominant plants; *Salicornia bigloveii* occurs along a salt-water runoff stream from the institute. A portion of this stream is fenced off for research purposes and includes open sand areas where ghost crab (*Ocypode quadrata*) burrows are evident. Although no tidal changes are present, infrequent interruptions of the seawater supply from the institute result in occasional desiccation of the stream bed.

Site IV is a mud-sand area of hurricane washover located between the Gulf beach back dunes and the main island road (Park Road 53), about 20 km. south of Port Aransas. Surface water is present in the form of several shallow ponds, but tidal changes are absent. Less clay and more sand is present than at site I, but soil moisture conditions and the general vegetation pattern are very similar. Flooding from heavy rains provides connections between the surface water and an adjacent artificial fish pass, which allows the influx of marine plankton, juvenile fish and small shrimp into the ponds.

The specific gravity of surface water at sites I and IV varies considerably, from 1.010 to 1.032, whereas water density at sites II and III is usually between 1.018 and 1.028 (measured by a hydrometer and checked with an optical refractometer).

FIDDLER CRAB DISPERSION

Rathbun (1918) reported *Uca pugilator* (Bosc) and *Uca pugnax* (Smith) from the Texas coast and these identifications have been repeated in recent works (Leary 1964; Felder 1973), including a preliminary report on Mustang Island fiddler crab ecology (Powers 1973). On the basis of ethological studies, Salmon and Atsaides (1968) identified 2 new species from the Gulf coast, *Uca longi-signalis* and *Uca virens*, that were formerly regarded as *Uca pugnax*; both are present on Mustang Island. In a similar study, Novak and Salmon (1974) distinguished *Uca panacea* as a separate species from *Uca pugilator*. Rao and Fingerman (1968) had previously pointed out differences in the chromatophore responses of "dimorphic variants of *Uca pugilator*" and Selander, Johnson and Avise (1971) indicated that the two forms were distinct on the basis of isozyme analysis. The amount of protein pattern differences for *U. pugilator* from several Atlantic coast areas was negligible in comparison to the distinct differences seen in Texas *U. panacea* populations (Robert Sealander, personal communication). Throughout this study and in others to follow (Powers 1975, and in preparation), the new species designations will be used. However, confirmation of these new

species by additional biochemical studies or breeding experiments would be highly desirable.

Uca panacea is by far the most common local species, occurring in a wide range of microbabitats, including cultivated lawns in Port Aransas more than a hundred meters from marshes or open surface water. The dispersion patterns for the three species are shown in Table 1. Substrate type and moisture are given in qualitative terms for the predominant conditions present at the site. Crab densities are based on counts of crabs active at the surface during summer days and represent 80–90% of actual densities as determined from excavations of meter-square quadrats to a depth of 35 cm. The excavated substrate was washed through a 0.2 cm. wire screen mesh and the retained crabs were counted.

Despite microhabitat preferences, the three species overlap in distribution at sites I, II, and III. At site I, *Uca panacea* inhabits the drier, sandier regions around patches of *Monathochloe*, whereas *U. virens* prefers to burrow in the wet mud of the algal flat, around clumps of *Salicornia*. Both species overlap at the *Spartina* zone, where moisture and substrate type are intermediate. *Uca longisignalis* is present at site II in small numbers at the base of *Spartina* clumps, along with the other two species. They are easily distinguished from *U. virens* by color and waving pattern (Salmon and Atsaides 1968). *Uca panacea* at site II is dispersed across the open sand flats (males, particularly) and among *Spartina* (females, particularly), whereas the other two species are almost always confined to zones of moderate to dense vegetation. *Uca panacea* is present in large numbers among *Spartina* at site III during the winter, but spreads into less vegetated areas and among *Salicornia* during the summer, presumably to facilitate display. *Uca virens* is present in a narrow band of dense grass around the runoff stream as it exits from an underground pipe; overlap occurs with *U. panacea* in nearby *Salicornia* clumps. Only *Uca panacea* has been found at site IV.

MOISTURE AND BURROW DEPTH

Fiddler crabs require periodic contact with a water source to resupply water lost by transpiration (Edney 1961). The crabs can extract water from the sub-

TABLE 1

Dispersion patterns for *Uca* on Mustang Island

Species	Site	Substrate	Max	Aver[1]	N[2]
U. longisignalis	II	dry-damp sand	5/m²	0.7/m²	40
U. panacea	I	damp-wet sand-mud	19/m²	5.3/m²	24
	II	dry-damp sand	26/m²	7.7/m²	40
	III	dry-damp sand	21/m²	9.7/m²	27
	IV	damp-wet sand-mud	24/m²	8.0/m²	16
U. virens	I	wet mud	34/m²	14.6/m²	24
	II	dry-damp sand	10/m²	6.2/m²	40
	III	damp-wet sand-mud	28/m²	19.1/m²	27

[1] Averages do not include quadrats containing 0 burrows or crabs.
[2] Number of m² quadrats sampled.

strate by capillary action, using branchial tuft hairs located between the second and third walking legs (Powers 1975). These hairs, upon contact with substrate moisture, conduct water to the pericardial sacs and then to the branchial cavities (see Bliss 1968 for a discussion of water uptake in other terrestrial crabs). Although *Uca virens* often digs holes to a depth sufficient to retain free water at the burrow terminal, *Uca panacea* burrows are almost always free of standing water. Sufficient water is present when the substrate is saturated (about 20% of wet weight, depending on particle size) to permit capillary extraction. In laboratory aquaria, where the surface is usually as damp as the bottom of the tank, crabs lower their abdomens to the surface substrate, press with a sideways movement, moistening the tufts in a second or less (Powers 1975). In deeper tanks, where the surface is dry but the bottom kept wet, the crabs return to their burrows periodically, as they do in the field.

Moisture or open water availability is probably the single most important factor limiting *Uca* distribution, especially for *Uca panacea* which otherwise occupies such a variety of microhabitats. Evidence to support this includes: 1) local migrations during the dry season occur at night and during early morning hours when ground moisture is maximal; 2) humidity and water availability are the most critical factors determining survival in the laboratory (Fig. 2); and 3) spatial patterns of *Uca* aggregations shift in response to changing water conditions

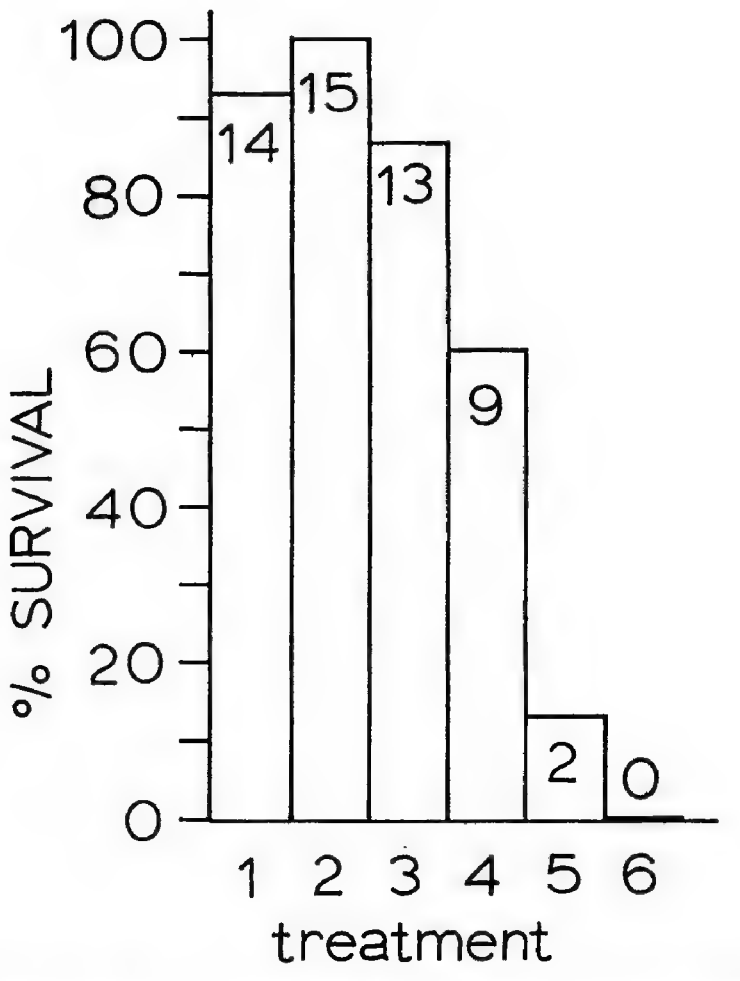

FIG. 2. Survival rates of male *Uca panacea* at different substrate moistures (water percent of total wet weight) at the end of five days. Temperature = 20–22 C. Treatments: 1—22.0%, 2—12.7%, 3—9.5%, 4—5.9%, 5—3.6%, 6—0.1%. Numbers inside bars indicate number of survivors of 15 animals for each treatment.

due to seasonal availability. *Uca* burrows at site I are located among the *Monathochloe*, *Juncus* and *Distichlis* patches of higher ground during the fall-winter rainy season, well away from flood ponds covering the adjacent algal flats. During the dry season, starting in April, shrinkage of the ponds and lowering of the adjacent water table results in deeper burrows and the relocation of burrows toward the ponds. By August, no standing water is seen at the surface, but recently-constructed burrows are scattered over the pond bed. Free water remains at a depth of 15–20 cm. below the surface. With the return of heavy rains and flooding of the algal flat, the crabs return to higher ground. Similar movements occur at sites II and III. Surface conditions may not be as important as substrate conditions near the burrow terminal as a stimulus for migration, because dry winter periods and infrequent heavy rains during the summer do not result in such displacements.

TIDAL FACTORS AT MUSTANG ISLAND

The local Gulf tides are predominantly diurnal, mixed, but the narrow passes filter out shorter period tidal components so that diurnal constituents are dominant in the inner waters, including the Corpus Christi Ship Channel (Smith 1974). Site II burrows can be regarded as supratidal in position, but water level measurements in the intracoastal bays and channels show a diurnal range of less than 4.6 cm. (0.15 feet).

In fact, meteorological factors contribute more to local water level variation than do astronomical factors, so that weather fronts can add to or subtract from the tidal amplitude. Thus, the arhythmic nature and small amplitude of water level changes influences *Uca* activity to a negligible extent.

TRANSLOCATION EXPERIMENTS

Intertidal populations of fiddler crabs were not found on Mustang Island, so in order to compare burrowing behavior under tidal and nontidal conditions, fifty *Uca panacea* (28 males, 22 females) were dug up at site IV (nontidal) and transported to the Corpus Christi Pass, about 2 km. south. Diurnal tidal inundation on a sandy beach bordering the pass and near the Gulf results in a 20-meter intertidal zone during spring tides. The crabs were released onto the exposed sand during low tide and confined within a 10 by 15 meter area (arena) surrounded by a temporary wood frame barrier. Within 5 hours and prior to coverage by the incoming tide, all but 6 males had dug burrows.

The barriers were left in place for one tidal cycle and removed at the next low tide. Counts of animals at the surface accounted for 35 crabs and at least 8 others were sealed inside burrows. Within 6 hours after removal of the barrier, 29 of the 35 surface active animals had moved into vegetation on higher ground some 30 meters inland from the arena. The remaining 6 crabs (5 were females) retreated into their intertidal burrows at approach of the rising water. Return visits on following days revealed that most of the crabs that had shifted to higher ground had burrowed among the *Spartina* (no other burrows were present prior

TABLE 2

Burrow-sealing behavior under different conditions

		SUBSTRATE MOISTURE			ILLUMINATION		DENSITY	
		Saturated	Wet	Damp	Light	Dark	4/Box	12/Box
TOTAL BURROWS	N =	303	88	214	510	740	192	1058
PERCENT SEALED	% =	40.9	10.2	2.3	13.9	36.4	24.5	27.7
Males	% =		not		8.9	29.8	15.6	22.3
			separated					
Females	% =		by sex		18.6	42.4	33.3	32.6

to the experiment); however, no crabs could be located in the arena area or adjacent intertidal zone.

Similar results were obtained on a smaller scale in the laboratory, using aquaria and manually changing the water level in relation to a sloped sand bank. *Uca panacea* occupied burrows at higher levels on the sand bank as the water level was raised slowly. When the entire sand surface was covered, crabs remained underwater and did not attempt to bury themselves in the sand. If inside a burrow during submersion, a crab remained in the burrow. Most crabs died if left underwater for more than three days (in 75% sea water).

BEHAVIORAL CONSEQUENCES

Unlike populations in the intertidal zone, nontidal *Uca* do not have to retreat into burrows every 6 or 12 hours because of approaching water. Most fiddler crabs seal their burrows from the inside (Fingerman 1957; Altevogt 1959), apparently in response to tidal inundation. *Uca panacea* rarely seals its holes when surface conditions are dry, but seasonal and sexual differences in the frequency of burrow sealing are seen in the field and can be experimentally confirmed in the laboratory. Saturated substrates result in an increase in sealed burrows by both males and females (Table 2). Transfer from the field to the laboratory or frequent disturbance of laboratory populations also results in increased frequencies of burrow plugging. Females show a greater tendency to seal burrows under all conditions. Sealing is pronounced when male crabs are crowded into small containers; sexual differences are most pronounced when crabs are placed under constant dark conditions (Table 2). During the winter, many burrows remain plugged for periods of many days to weeks with the crabs inactive due to cold temperatures. In the summer, with conditions favorable for surface activity throughout the day and night, 92–96% of the burrows remain open.

The total display and surface feeding time of local, nontidal populations is potentially twice that of intertidal populations. Because of the elimination of frequent burrow repairs due to water damage, the increased time available may be as high as three or four times greater. Although intertidal crabs were not available for comparison, observations of marked nontidal crabs (acrylic paint spots on the dorsal carapace, protected by fingernail varnish) reveal that individual crabs do utilize most of this time in display (males) and feeding (males and fe-

TABLE 3

Burrow and crab densities

Site	m^2	No. of burrows	Density	No. of crabs	Density	Crabs per hole
I	8	140	17.5/m^2	58	7.25/m^2	.414
II	12	185	15.4/m^2	83	6.93/m^2	.449
Total	20	325	16.3/m^2	141	7.05/m^2	.434

males), and remain active throughout the entire daytime during the summer. During warm winter days, long periods of feeding and posturing at the burrow mouth are seen. Depending on the surface temperature, crabs spend from about 5 to 30 minutes outside of the burrow on each excursion, interspersed with 1- to 3-minute periods inside the burrow to replace water lost by transpiration (Powers, in preparation). The relationship between temperature and excursion time is influenced by other factors, such as sex of crab, season and nature of social interactions during excursions.

An additional consequence of burrow semi-permanence is the availability of a surplus of burrows for refuge when intruders or potential predators appear. As Table 3 indicates, there are more than two crab burrows for every crab so that ready access is possible when crabs are wandering, feeding or fighting away from their own burrows. Laboratory observations of burrow frequency indicate that this number of burrows/crab is relatively constant, due in large part to extra holes dug by females. During peak aggressive phases of males, whether during courtship times or not, females may dig 4 or 5 burrows in succession, only to be displaced from each hole by a wandering male as the burrow nears completion. When the female does finish a burrow under these conditions, she usually seals herself inside for 12 hours or more. Detailed results of studies on burrow occupancy and use of space by fiddler crabs is in preparation, in addition to Powers (1975).

DISCUSSION

Uca panacea has not been adequately studied in the field in intertidal zones or at other points in its range. The same applies to the other two species on Mustang Island, which are more nocturnal in habits and do not habituate to the presence of an observer as readily as does *U. panacea*. Clearly, detailed comparisons between intertidal and nontidal populations, preferably in proximity to each other, will be needed to make meaningful hypotheses on the ecological and behavioral consequences of these different habitats. We can, however, speculate on some of the possible effects of burrow stability on the evolution of social behavior. Other semiterrestrial and terrestrial crabs that burrow at greater distances from the high tide mark, such as *Ocypode quadrata*, return to feed at the drift line, leaving the burrow vicinity. These animals do not aggregate in clusters as is seen in *Uca* and social relationships are mainly confined to courtship and mating (Cowles 1908; Milne and Milne 1946; Linsenmair 1967). Barrass (1963) reports aggre-

gations of *Ocypode* due to crowding in a narrow habitat, but he does not indicate whether significant behavioral differences are present in these populations. *Ocypode* and *Gecarcinus* are predominantly nocturnal and tend to be dispersed over a broad area, as compared to the clustering pattern of *Uca* colonies in nontidal areas. *Ocypode* does not display the elaborate rituals and frequent interactions observed in various *Uca* species (Crane 1957, 1966, 1967). Thus, nontidal *Uca* have moved inland to habitats where superdispersion could follow the pattern seen in land crabs, but the gregarious behavior of fiddler crabs leads to a spatial pattern similar to nontidal populations (Powers 1975). Observations of *U. panacea* and *U. virens* indicate that the full range of courtship activities, combat rituals and other social interactions are present and that tidal synchronization of activity time is not necessary to facilitate contact.

When tidal changes are not present, other environmental cues may be substituted as *zeitgebers*. Altevogt (1959) compared intertidal and nontidal populations of *Uca tangeri* and found that the latter did not show signs of tidal rhythmicity, even though in close proximity to the intertidal crabs. The nontidal crabs were diurnal and activity was triggered in the morning and evening. Land crabs, such as *Gecarcinus* and *Cardisoma* also lack spontaneous tidal rhythms (Palmer 1973), but green crabs (*Carcinus maenas*) from essentially nontidal habitats, which initially show no tidal rhythmicity, exhibit tidal rhythms after exposure to a brief cold pulse (Naylor 1960, 1963). *Uca pugilator* loses its tidal rhythm after about a month in constant conditions of light and temperature (Barnwell 1966). Thus the persistence of tidal rhythms, however innate their basis, appear to require periodic reinforcement, a factor lacking in Mustang Island *Uca*. Whether adaptations to nontidal habitats can become genetically fixed or not is yet to be determined.

Fiddler crabs are capable of fairly complex behavior and learning performances (Schone 1961, 1965), yet they have achieved a social stage barely higher than gregarious, with no signs of cooperative behavior. Planktonic larval dispersal seems to rule out the evolution of higher social orders via kin selection, but nontidal ponds that are suitable for larval survival and maturity could localize a small gene pool and perhaps favor kin selection.

Synchronization of activities over a short time period, such as claw-waving in African intertidal *Uca* (Gordon 1958), is a common social behavior seen in crabs. Movements of some crabs tend to facilitate movements of nearby crabs, seen to the extreme in the soldier crab of Australia, *Mictyris longicarpus* (Cameron 1966). In both laboratory and field, facilitation of feeding, waving and movement are seen in *Uca panacea* and *U. virens*. Several males initiated the inland movements during the translocation experiment, followed by other crabs in groups of 5 and 10. Mass movements or "promenading" behavior, seen in many intertidal populations (Crane 1943, 1958; Hockett and Kritzler 1972), is not seen in Mustang Island *Uca*, possibly due to the lack of activity synchronization by tides. During the summer, *Uca panacea* is active day and night and individual activity periods (observed in marked animals) vary considerably in duration and time of occurrence (Powers 1975).

The location of burrows away from the intertidal zone also changes predator-prey relationships. Teal (1958) lists various *Uca* predators in Georgia marshes, including blue crabs, mud crabs, fish, birds and racoons. All of these are opportunistic feeders that do not rely on *Uca* for a substantial portion of their diets. Away from water, the major Mustang Island predators are birds (herons, egrets, cranes, gulls and terns), ghost crabs and man (*Uca* are dug for fishing bait). Several species of lizards and snakes are found in burrow areas, but no evidence indicates that these animals feed on *Uca*. Crichton (1960) states that *Sesarma reticulatum*, the marsh crab, preys on *Uca* where burrows overlap. *Sesarma* occurs supratidally with *U. panacea* at site II and the two species have been observed together on the surface during warm summer nights, but the predatory status of *Sesarma* has not been verified, either in the field or in mixed populations kept in the laboratory. *Uca panacea* shares burrows with many other arthropods (Bright and Hogue 1972 review the literature), especially ground spiders. Fiddler crabs are also opportunistic feeders, and though the major share of their diet consists of algae and other microorganisms scraped from sand particles, *Uca panacea* has been observed to catch june bugs, beetles, and cockroaches and devour them avidly (Powers 1975).

In summary, the differences between nontidal and intertidal populations of fiddler crabs may include many behavioral and ecological adaptations, some of which have significance for the social evolution of these gregarious animals. Specific differences in the spatial patterns of burrows, their utilization and the social relationships among crabs need to be analyzed for each major type of habitat occupied. Such an analysis is now underway for the western Gulf populations of *Uca panacea* (Powers, in preparation) with the goal of developing a life history model that encompasses and correlates diverse ecological and behavioral data. By comparing similar models derived from studies of other, closely-related species, the key determinants of social evolution in fiddler crabs may become apparent.

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SEASONAL AND AREAL COMPARISONS OF FISH DIVERSITY INDICES AT A HOT-WATER DISCHARGE IN GALVESTON BAY, TEXAS

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ABSTRACT

Trawl and hydrological samples were taken at 11 stations once each month January 1968 through December 1969 in an area of Galveston Bay receiving a discharge of heated water from the P. H. Robinson Generating Station. The stations were grouped by location into three areas: 1) an up-bay control area, 2) the discharge area and 3) a down-bay control area. The data from stations in each of the three areas were pooled and three diversity indices, the Shannon-Weaver index (H″), evenness (J) and species richness (D), were calculated for each monthly sample. Analysis of all indices showed marked seasonal differences. No significant differences in overall diversity (H″) or evenness indices were observed between years or areas. The species richness index for 1968 was significantly higher than that for 1969 and the discharge area had significantly greater species richness than either control area. The greater species richness in the discharge area may have been related to sample size. In the discharge area, all indices declined when mean surface water temperature was above 35C.

INTRODUCTION

The effects of hot-water discharges from steam electrical generating stations (s.e.s.) on estuarine fish populations as determined with the aid of diversity indices have been little reported. The use of diversity measures to analyze estuarine fish populations has only recently surfaced in the literature. Bechtel and Copeland (1970) found species diversity indices calculated for both fish weights and numbers from trawl collections were useful indicators of environmental stress in Galveston Bay, Texas and demonstrated that the concept of using species diversity to indicate adverse water quality conditions was applicable to the higher trophic levels of an estuary. Based on fish data from a trawl study in a Georgia estuary, Dahlberg and Odum (1970) suggested that the use of a combination of indices was desirable in order to separate the two components of diversity, "species richness" and relative species abundance. Grimes (1971) used the diversity index $(S-1)/\log_n N$ to compare species diversity of fishes at stations of increasing distance from the point of a discharge in Crystal River, Florida and noted slight shifts in diversity toward the discharge in winter and away from the discharge in summer. McErlean *et al.* (1973), reporting on data gathered from

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the Patuxent Estuary in Maryland, compared several diversity indices and noted occasional temporal shifts but no marked effects on fish populations due to s.e.s. activities.

Gallaway and Strawn (1974) have provided data concerning fish populations at the mouth of the P. H. Robinson Generating Station's discharge in Galveston Bay, Texas. Based on data from a two-year trawl we found that the highest species-per-trawl-haul value occurred at the effluent mouth and was significantly different at the 5% level from all other values. In the same paper, we evaluated the effects of the discharge on the 10 most abundant fishes in the receiving area of the effluent and compared abundance and occurrence of these fishes in the discharge area at 900 megawatt (Mw) generating capacity with those at 1465 Mw. The selected species comprised 98% of the total catch (all gear types combined) which contained representatives of 89 species.

This paper compares species diversity indices through two annual cycles of fishes trawled in the discharge area of the P. H. Robinson Generating Station to those in both up- and down-bay control areas.

STUDY AREA AND METHODS

The P. H. Robinson Generating Station, operated by the Houston Lighting and Power Company, is located on a 486 ha site near Bacliff, Texas on State Highway 146. The plant began operations in 1966 with one 450 megawatt (Mw) generating unit which pumped about 12.6 m^3/sec of cooling water. During the study period, two 450 Mw generating units were operational both years and a 565 Mw generating unit was completed in November 1968. Together these units were capable of pumping as much as 41 m^3/sec of cooling water through the plant's designed 9.8 C maximum rise condensers. A fourth unit of 750 Mw capacity began operation in 1973.

The plant received cooling water for the main condensers from Dickinson Bay through a 3.7 km intake canal. The discharge canal was approximately 3.2 km long and entered Galveston Bay between Bacliff and San Leon, Texas.

Trawl and hydrological samples were taken one each month from January 1968 through December 1969 at 11 shallow water stations distributed among three separate areas (Gallaway and Strawn 1974) as described in Table 1. Each area contained stations of equivalent depths and distances from shore. Trawl collections were made at night and consisted of a three-minute trawl tow at each station with a 6.1 m wide Texas-balloon trawl having 3.8 cm stretched mesh in the body and 2.5 cm stretched mesh in the cod end. A 4.8 mm stretched mesh cover was fitted over the cod end of the trawl to capture small specimens.

Except for March of 1969, trawl collections were made each month at all offshore stations. In March 1969, we were forced to trawl during the day because of an approaching storm and were able to make collections at only four stations (3, 5, 8 and 11).

Bechtel and Copeland (1970), applying the Shannon-Weaver diversity index to Galveston Bay fish data, determined that indices based on pooled data were probably more representative of an area than the mean of areal indices based on single collections. Data from stations in each of the three areas were pooled by area and analyzed as a single collection. In our study, stations 1–3 and 9–11 represented the up- and down-bay control areas, respectively, and stations 4–8 represented the discharge area.

The Shannon-Weaver index was selected as the best overall index of diversity because it is reasonably independent of sample size and normally distributed (Bowman *et al.* 1970). Collection data were tabulated by number of species and number of individuals and the index was estimated following Pielou (1966a):

$$H'' = -\Sigma \frac{n_i}{n} \log_e \frac{n_i}{n}$$

TABLE 1

Areal grouping, distance offshore, depth, and substrate of trawl stations at the P. H. Robinson Generating Station, Galveston Bay, Texas

STATION	AREA	DISTANCE OFFSHORE (m)	DISTANCE FROM OUTFALL (km)	AVERAGE DEPTH (m)	SUBSTRATE
1	Up-Bay Control	185	2.1	1	Packed Sand
2	Up-Bay Control	370	2.1	1	Packed Sand
3	Up-Bay Control	555	2.1	2	Mud and Sand
4	Discharge	185	0.2	1	Silt and Mud
5	Discharge	(Canal mouth)	0.0	3	Silt and Mud
6	Discharge	185	0.2	1	Silt and Mud
7	Discharge	370	0.4	1	Silt and Mud
8	Discharge	555	0.6	2	Silted-over oyster reef
9	Down-Bay Control	185	1.9	1	Packed Sand
10	Down-Bay Control	370	1.9	1	Sand and Shell
11	Down-Bay Control	555	1.9	2	Live Oyster Reef

where n_i is the number of individuals in the i^{th} species and n is the total number of individuals in the collection.

One advantage of the Shannon-Weaver index is that it is possible to compare H″ to its upper theoretical maximum. This measure is related to redundancy and can be used to measure dominance or how evenly numbers are allocated in species categories by comparison with the calculated maximum. The "evenness" index of Pielou (1966b) was calculated:

$$J = H''/H_{max} = H''/\log_e S$$

in which $\log_e S$ is the maximum possible value of H″.

Following Dahlberg and Odum (1970) the species richness aspect of diversity was calculated for each pooled sample:

$$D = S\text{-}1/\log_e N$$

where S is the number of species and N is the number of individuals. This index is influenced by sample size. Except for March 1969, discharge area samples consisted of 15 minutes effort and samples from each control area consisted of 9 minutes effort. March 1969 comparisons were based on 6 versus 3 minutes of trawling.

Factorial analysis of variance was performed for each index and F values calculated to partition the total variation into its various sources: areas, months, years, area by month interaction, area by year interaction and month by year interaction. The sources of variation were considered significant if calculated F values were significant at the 5% level.

RESULTS

A total of 68 species representing 32 families were trawled during the 2-year study (Table 2). Of these, representatives of 5 species comprised about 95% of the catch and 16 species were represented by a single specimen. The 1968 catch

TABLE 2

Species and number trawled each year shown in order of total abundance

SPECIES	1968	1969	TOTAL
Micropogon undulatus	22,593	16,541	39,134
Anchoa mitchilli	7,790	19,655	27,445
Arius felis	4,781	9,937	14,718
Brevoortia patronus	2,154	2,983	5,137
Polydactlus octonemus	3,067	646	3,713
Cynoscion arenarius	443	824	1,267
Leiostomus xanthurus	570	462	1,032
Menticirrhus americanus	148	286	434
Symphurus plagiusa	186	210	396
Prionotus tribulus	59	77	136
Bagre marinus	100	34	134
Sphoeroides parvus	13	113	126
Chaetodipterus faber	104	16	120
Mugil cephalus	67	46	113
Myrophis punctatus	53	40	93
Achirus lineatus	38	40	78
Gobiosoma bosci	45	21	66
Dorosoma cepedianum	34	28	62
Stellifer lanceolatus	50	4	54
Ophichthus gomesi	12	38	50
Opsanus beta	24	21	45
Citharichythys spilopterus	11	28	39
Chloroscombrus chrysurus	36		36
Ophilion welshi	14	17	31
Birdiella chrysura	12	10	22
Etropis crossotus	1	19	20
Astroscopus y-graecum	12	6	18
Dorosoma petenense	12	1	13
Porichthys porosissimus	12		12
Sciaenops ocellata	12		12
Pogonias cromis	7	4	11
Gobionellus boleosoma	1	9	10
Gobiosoma robustum	9	1	10
Paralichthys albigutta		10	10
Trinectes maculatus	1	9	10
Gobiesox strumosus	3	5	8
Citharichthys macrops	8		8
Urophycis floridanus	3	4	7
Paralichthys lethostigma	5	1	6
Trichiurus lepturus	1	5	6
Peprilus burti	5		5
Cyprinodon variegatus	4		4
Membras martinica	1	3	4
Caranx-hippos	2	2	4
Peprilus alepidotus	2	2	4
Cynoscion nebulosus	2	1	3
Harengula pensacolae	1	1	2
Oligoplites saurus	2		2
Eucinostomus argenteus	2		2

TABLE 2—Continued

SPECIES	1968	1969	TOTAL
Eucinostomus gula	2		2
Eucinostomus lefroyi	2		2
Lagodon rhomboides		2	2
Dasyatis sabina	1		1
Elops saurus	1		1
Mystriophis intertinctus	1		1
Opisthonema oglinum	1		1
Cyprinus carpio	1		1
Ictalurus melas		1	1
Syngnathus scovelli		1	1
Lepomis cyanellus	1		1
Lepomis megalotis		1	1
Caranx latus	1		1
Trachinotus carolinus		1	1
Archosargus probatocephalus	1		1
Evorthodus lyricus		1	1
Gobioides broussonneti	1		1
Ancylopsetta quadrocellata	1		1
Lagocephalus laevigatus		1	1

contained representatives of 20 species that were not trawled in 1969 and the 1969 catch contained representatives of 8 species that were not caught in 1968. Most of the species trawled one year but not the other represented a few specimens (Table 2). Four freshwater species (*Cyprinus carpio, Ictalurus melas, Lepomis cyanellus, Lepomis megalotis*) were trawled.

Monthly abundance levels (catch/trawl tow) were seasonal and the catches were usually dominated by one or two species which changed with season (Table 3). The largest collections during 1968 were made during January–June and September. The largest collections of 1969 were trawled during February–August and November. Winter (December–February) collections were dominated by either *Micropogon undulatus, Anchoa mitchilli* and/or *Brevoortia patronus* (Table 3). Spring collections were dominated by *Micropogon undulatus* and/or *Anchoa mitchilli.* These species were also among the dominants during early summer (June) with *Arius felis* and/or *Polydactylus octonemus* becoming more abundant during middle and late summer (July–August). *Arius felis, Brevoortia patronus* and/or *Anchoa mitchilli* dominated fall (September–November) catches. Except for *Anchoa mitchilli* which matures early and has a short life span, most of the individuals representing the respective dominant species during a given season were apparently immature young-of-the-year fish (Gallaway and Strawn 1974).

Results of the analysis of variance tests performed on the Shannon-Weaver indices (Table 4) and the evenness indices (Table 5) gave similar results. No significant differences were indicated between years, areas, areas by month or areas by year. Significant differences were indicated for months and month by year interaction. Monthly values of the mean for each index were graphed by

TABLE 3

Monthly abundance, number of species, and dominant species trawled during January 1968–December 1969

Month	Fish/trawl	No. Species	Dominant Species	% Catch
1968				
Jan	394	25	*Micropogon undulatus*	78
Feb	326	21	*Micropogon undulatus*	85
Mar	291	19	*Micropogon undulatus*	89
Apr	870	20	*Micropogon undulatus*	78
May	448	17	*Micropogon undulatus*	64
Jun	416	22	*Micropogon undulatus*	37
			Polydactylus octonemus	30
Jul	191	23	*Anchoa mitchilli*	41
			Micropogon undulatus	24
Aug	227	23	*Arius felis*	66
Sep	429	23	*Arius felis*	44
			Brevoortia patronus	23
			Anchoa mitchilli	22
Oct	183	24	*Anchoa mitchilli*	64
Nov	61	24	*Anchoa mitchilli*	37
			Brevoortia patronus	36
Dec	30	16	*Micropogon undulatus*	35
			Anchoa mitchilli	22
1969				
Jan	79	19	*Micropogon undulatus*	69
Feb	558	20	*Brevoortia patronus*	41
			Micropogon undulatus	35
Mar	972	11	*Micropogon undulatus*	95
Apr	980	16	*Anchoa mitchilli*	53
			Micropogon undulatus	45
May	796	18	*Anchoa mitchilli*	65
Jun	375	19	*Micropogon undulatus*	49
			Anchoa mitchilli	31
Jul	450	22	*Arius felis*	84
Aug	421	21	*Arius felis*	83
Sep	153	22	*Arius felis*	72
Oct	95	24	*Arius felis*	48
			Anchoa mitchilli	25
Nov	407	22	*Anchoa mitchilli*	92
Dec	75	22	*Anchoa mitchilli*	51
			Micropogon undulatus	27

year (not shown) and the differences compared. The mean H″ values for January–September periods were fairly similar (average of differences was 0.245) but October–December data were quite different between years (mean of differences was 0.733). The greatest difference between monthly means of H″ (1.148) occurred in November (Table 4). The November 1968 collection contained 24 species represented among 694 specimens. In contrast, although 22 species were trawled in November 1969, 4,476 specimens were collected. Of these, 4,126 were *Anchoa mitchilli*.

The graph for month by year evenness values (J) showed a pattern similar to the graph for species diversity. The mean evenness values for January-September were similar between years (mean of differences was 0.109) while those for October–December were markedly different (mean difference was 0.285). The greatest difference occurred during November (Table 5) and was caused by the great abundance of *Anchoa mitchilli* in the 1969 collections.

Results of the analysis of variance performed on the monthly species richness

TABLE 4

Shannon-Weaver diversity indices based on trawl data, January 1968–December 1969. (UBC = Up-bay control, stations 1–3; Da = Discharge area, stations 4–8; DBC = Down-bay control, stations 9–11.)

	INDICES							
	1968				1969			
Months	UBC	DA	DBC	MEAN	UBC	DA	DBC	MEAN
Jan	0.823	0.663	0.596	0.694	1.116	1.190	0.831	1.046
Feb	0.839	0.548	0.433	0.607	0.904	0.993	1.005	0.967
Mar	0.364	0.564	0.564	0.497	0.508	0.306	0.464	0.427
Apr	0.941	0.774	0.578	0.764	0.863	0.845	0.683	0.797
May	1.455	1.142	0.872	1.156	0.682	1.215	0.780	0.892
Jun	1.315	1.480	1.311	1.369	0.980	1.373	1.062	1.138
Jul	1.516	2.051	1.243	1.603	1.736	0.530	1.164	1.143
Aug	1.343	0.669	1.328	1.113	0.880	0.446	1.213	0.846
Sep	0.768	1.269	1.273	1.103	1.380	0.779	1.664	1.274
Oct	0.433	1.679	0.938	1.017	1.357	1.482	1.963	1.601
Nov	1.594	1.593	1.692	1.626	0.179	0.996	0.260	0.478
Dec	1.021	2.044	1.378	1.481	0.018	1.667	1.357	1.014
Areal Mean	1.034	1.206	1.017		0.967	0.985	1.037	
Yearly Mean		1.086				0.996		

TABLE 5

Evenness indices based on trawl data, January 1968–December 1969. (UBC = Up-bay control, stations 1–3; DA = Discharge area, stations 4–8; DBC = Down-bay control, stations 9–11.)

	INDICES							
	1968				1969			
Months	UBC	DA	DBC	MEAN	UBC	DA	DBC	MEAN
Jan	0.331	0.221	0.226	0.259	0.508	0.439	0.464	0.470
Feb	0.431	0.190	0.169	0.263	0.364	0.387	0.371	0.374
Mar	0.187	0.203	0.227	0.206	0.366	0.139	0.335	0.280
Apr	0.428	0.268	0.225	0.307	0.393	0.329	0.351	0.358
May	0.606	0.422	0.340	0.456	0.310	0.507	0.296	0.371
Jun	0.571	0.512	0.511	0.531	0.446	0.485	0.443	0.458
Jul	0.610	0.739	0.471	0.607	0.658	0.187	0.411	0.419
Aug	0.509	0.247	0.490	0.415	0.343	0.157	0.460	0.320
Sep	0.291	0.424	0.449	0.388	0.576	0.275	0.587	0.479
Oct	0.188	0.551	0.391	0.377	0.566	0.495	0.725	0.595
Nov	0.604	0.541	0.641	0.595	0.072	0.338	0.099	0.170
Dec	0.634	0.775	0.856	0.755	0.490	0.577	0.566	0.544
Areal Mean	0.449	0.424	0.416		0.424	0.360	0.426	
Yearly Mean		0.430				0.403		

indices (Table 6) showed significant differences between areas, months, years and month by year interaction. A Duncan Multiple Range Test showed all three areas to have been significantly different in terms of the species richness index. The areas were ranked from high to low species richness: 1) discharge area, 2) down-bay control area, and 3) up-bay control area. Species richness was higher in 1968 than in 1969. Monthly values between years were unduly divergent only during March and November.

TABLE 6

Species richness indices based on trawl data, January 1968–December 1969.
(UBC = Up-bay control, stations 1–3; DA = Discharge area,
Stations 4–8; DBC = Down-bay control, stations 9–11.)

	INDICES							
	1968				1968			
Months	UBC	DA	DBC	MEAN	UBC	DA	DBC	MEAN
Jan	1.553	2.415	2.071	2.013	1.599	2.222	0.965	1.595
Feb	0.902	2.315	1.680	1.632	1.346	1.560	2.325	1.744
Mar	0.908	1.984	1.746	1.546	0.447	1.002	0.612	0.687
Apr	1.039	2.049	1.478	1.522	1.038	1.487	0.699	1.075
May	1.614	1.729	1.701	1.681	1.042	1.279	1.562	1.294
Jun	1.380	2.107	1.835	1.774	1.140	2.059	1.550	1.583
Jul	1.644	2.325	2.002	1.990	2.381	1.921	2.521	2.274
Aug	2.025	1.932	2.270	2.076	1.764	1.990	2.022	1.925
Sep	1.988	2.321	2.623	2.311	1.693	2.300	2.873	2.289
Oct	1.300	3.052	1.738	2.037	1.749	2.980	2.765	2.498
Nov	2.619	3.011	2.650	2.760	1.442	2.608	1.790	1.947
Dec	0.994	2.609	0.819	1.474	1.238	2.884	1.930	2.017
Areal Mean	1.497	2.321	1.886		1.407	2.024	1.801	
Yearly Mean		1.901				1.744		

DISCUSSION

We observed a net reduction of 12 species between years and the annual mean for each index decreased in 1969 from that observed in 1968. Analysis showed only the species richness differences were significant. More years would be needed to determine whether the observed differences were related to cyclic phenomena or to a trend of diversity reduction due to environmental degradation.

The monthly diversity values, although different between years, did show definite seasonal trends (Tables 4–6). The highest mean of monthly values for all three indices during winter occurred during December. Diversity values usually decreased from December levels through March and then began a steady increase through July. July diversity levels were followed in all cases by a sharp decline in August. The indices were highly variable during fall months with values occurring at or near the observed maximum and minimum levels. Based on quarterly sampling, Bechtel and Copeland (1970) observed that winter and spring seasons in Galveston Bay exhibit the lowest diversity with an increase occurring into the fall.

Most of the effects on diversity of trawled fishes observed during this study were life history effects and primarily related to the seasonal abundance and habitat preferences of the three most abundant species, *Micropogon undulatus*, *Anchoa mitchilli* and *Arius felis*. Diversity (H″) and evenness (J) values were generally low in all of the areas during winter and early spring because of the abundance of young *Micropogon undulatus*, and at some point during the fall, because of *Anchoa mitchilli* abundance. The seasonal abundance of young *Arius felis* usually suppressed these indices during some late summer and early fall months. Effects from *Micropogon undulatus* and *Arius felis* abundance were somewhat pronounced in the discharge area where these fishes were observed to concentrate, and effects related to *Anchoa mitchilli* abundance were pronounced in the control areas as this species generally avoided the discharge area (Gallaway and Strawn 1974).

Although the areal differences were not significantly different, the values for H″ were markedly lower in the discharge area than in the control area values during August 1968 and July–September 1969. The discharge area mean water temperature during these months and June 1969 exceeded 35C. Mean water temperature in control areas during the same months did not exceed 32C. Species diversity in the down-bay control areas usually exceeded that observed for the up-bay control area (Table 4). Oyster reef substrates provided habitats in the down-bay area that were not available in the up-bay environment.

The discharge area had greater species richness than either of the control areas. This difference may have been an artifact of unequal sample size. However, previous analysis based on equal effort did show station 5, the discharge mouth, to have had significantly more species present than any of the other stations (Gallaway and Strawn 1974).

SUMMARY

Fish species diversity in the sampled area of Galveston Bay exhibited seasonal trends and was strongly affected by the monthly abundance patterns of the three dominant species, *Micropogon undulatus*, *Anchoa mitchilli*, and *Arius felis*. Comparison of the discharge area to the two control areas in terms of diversity indices did not indicate significant differences. Temporary reductions in diversity were observed when mean surface water temperatures exceeded 35C. The species

richness aspect of diversity appeared to have been higher in the discharge area than in either of the control areas during both years.

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SUMMER GROWTH DEPRESSION IN THE STRIPED MULLET, *MUGIL CEPHALUS* L.

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ABSTRACT

Growth rates by scale analysis of *Mugil cephalus* taken from south Texas coastal waters throughout one year showed two major periods of slow growth. The period of slowest growth, followed by annulus formation, occurred during the colder late autumn and winter months. Another major growth depression occurred during the summer when food availability to the mullet should be maximal. Optimal growth rates for Age I and older fish were in spring and briefly in early autumn. Annual growth increments, however, agree well with those for other published Gulf of Mexico mullet studies. Females appear to be slightly, but not significantly, larger and to have somewhat better survival rates. The summer growth rate depression coincides with observations of pronounced summer depression of active and routine respiratory rates observed in earlier studies. This coincidence implies that there may be unknown summertime changes in food assimilation and in biochemical metabolic pathways. The summer growth rate depression would have significant effects on assessments of biological production rates compared to similar assessments conventionally based on yearly increments.

INTRODUCTION

The purpose of this study was to determine the growth rate of striped mullet, *Mugil cephalus* L., along the south Texas coast as part of an investigation of physiological responses to seasonal temperatures throughout the year (Cech 1973). The growth rate of fishes is commonly influenced by temperature and food ration (Brett 1970a, b; Gerking 1966, 1972; Ricker 1958; Thomson 1951; Warren and Davis 1967; Winberg 1956; among others). The fact that growth patterns and rates in fishes are generally known to be very sensitive to biotic and abiotic stresses provides a basis for both theoretical and practical insight into the nature of both functional adaptations and population dynamics. This sensitivity is especially useful when growth constitutes an important non-maintenance energy cost in fishes (Warren and Davis 1967), because growth rate information adds to a more complete understanding of energy budget allocations in response to natural environmental stimuli at different times of the year. Also, population modeling should take into account the influence of data-based information on erratic seasonal growth and metabolic variations.

The striped mullet is a euryhaline, eurythermal teleost found worldwide throughout coastal tropical, subtropical and warmer temperature areas (Broad-

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head 1958). It is one of the most common species along the Texas Gulf of Mexico coast (Gunter 1945), where its annual growth pattern from this study agrees well with earlier local studies by Hellier (1962) and with other Gulf of Mexico populations studied by Anderson (1958), Broadhead (1958), Shireman (1965), and others, if modest allowance is made for environmental differences in the various localities. However, in both brackish and marine coastal waters in south Texas the summer total metabolic rates, adjusted for size, swimming speed and salinity had a pronounced depression when compared to late spring or early autumn levels at lower temperatures (Wohlschlag and Moore 1973, ms.). Further, about 80% of the same mullet, both mature and immature, had pronounced evidence of summer false annuli in their scale growth patterns which also suggests a decline in summer growth. Because no gross environmental disturbances that could have caused major summer metabolic or growth declines were evident and because the growth component of total metabolism can be large, this study was undertaken to determine whether the earlier observed summer metabolic depression would be accompanied by a summer growth depression.

METHODS

Specimens were captured wherever plentiful by either seine or cast net in 40 collections that were taken throughout the year from Copano and Redfish Bays, Aransas and Corpus Christi Passes, and the Gulf beaches of Mustang and St. Joseph Islands. Although all the collections were within about 24 km from the Marine Science Institute, Port Aransas, Texas, the great complexities of local environments and mullet distribution did not necessarily permit the assumption of randomization. Several fish from each collection were acclimated in the laboratory for 1–3 days for physiological measurements (Cech 1973). At the end of the experiments, the fish were weighed, measured and sexed; scales were removed from the humeral area approximately at the distal end of the left pectoral fin.

The validity of the scale growth patterns for aging *Mugil cephalus* is widely known from work by Thomson (1951) and Broadhead (1958), among others. Impressions of the scales on heated plastic microscope slides by means of a hydraulic press provideed clear indications of growth patterns when magnified 40 times by a scale projector. The magnified scale images permitted counts of the annuli and measurement of anterolateral radii to the annuli and to the edge of each scale. Approximate back calculations of standard lengths (from snout to end of hypural plate) were made by use of the Lee (1920) formula,

$$L_n = a + \frac{V_n\,(L - a)}{V_r},$$

where,

L = standard length of fish at capture,
L_n = calculated standard length at n years,
V_r = anterolateral length of scale from focus to edge,
V_n = anterolateral length from focus to n^{th} annulus, and
a = approximate standard length at time of scale formation, 9.1 mm.

The value for a was the intercept taken from the regression equation relating body length to scale length:

$$L = a + b\,V_r.$$

RESULTS

Table 1 illustrates conveniently how the mean back calculated standard lengths increase with age, but with the usual decrease in annual growth incre-

TABLE 1

Mean back-calculated standard lengths in millimeters

Age Class	(n)*	Standard Lengths (mm) I	II	III	IV	V
1+	(39)	132				
2+	(71)	127	194			
3+	(54)	122	188	234		
4+	(12)	125	178	227	266	
5+	(3)	127	183	213	249	286
Means		127	186	225	258	286
Growth Increments		59	39	33	28	

*n = Sample size in each age class.

TABLE 2

Back-calculated standard lengths for male and female *Mugil cephalus* ± 1 standard error. Sample size in parentheses

Age	Males	Females
I	139 ± 4 (21)	146 ± 10 (3)
II	191 ± 3 (34)	197 ± 3 (36)
III	229 ± 4 (30)	240 ± 4 (24)
IV	262 ± 7 (4)	269 ± 10 (8)
V	—	286 ± 8 (3)

ments with age. The difference in growth rates between males and females (Table 2) is small and statistically not significant, although the average female tends to be somewhat larger. It is possible that the females may have higher survival rates.

Within the year, however, irregularity in growth pattern is apparent when the growth rate is plotted as the difference between the standard length at capture and the back-calculated standard length from the most recent annulus for fish caught throughout the year. In Fig. 1 these average differences are plotted for ten individuals ± 2 standard errors, each ten selected by chronological proximity. On a statistical basis for all age groups, the usual pattern would be increasing spring to summer increments with leveling off by autumn and with minimal increments from late November to late February, at which time annulus formation obviously occurs for the mullet in this area. Fig. 1 indicates clearly, however, that there is a pronounced tendency for the increments to level off during the June–August period followed by a brief period of increased increments. The sole collection group containing only small mullet in age classes 0 and I is indicated by asterisk in Fig. 1; these small fish have exceptionally large growth increments in September.

Statistical analyses by means of the t-test (*e.g.*, Snedecor and Cochran 1967) reveal no significant difference between April–May growth increments and those for June–July–August, no difference between June–July–August increments and those for October–November, but a definite difference between the June–

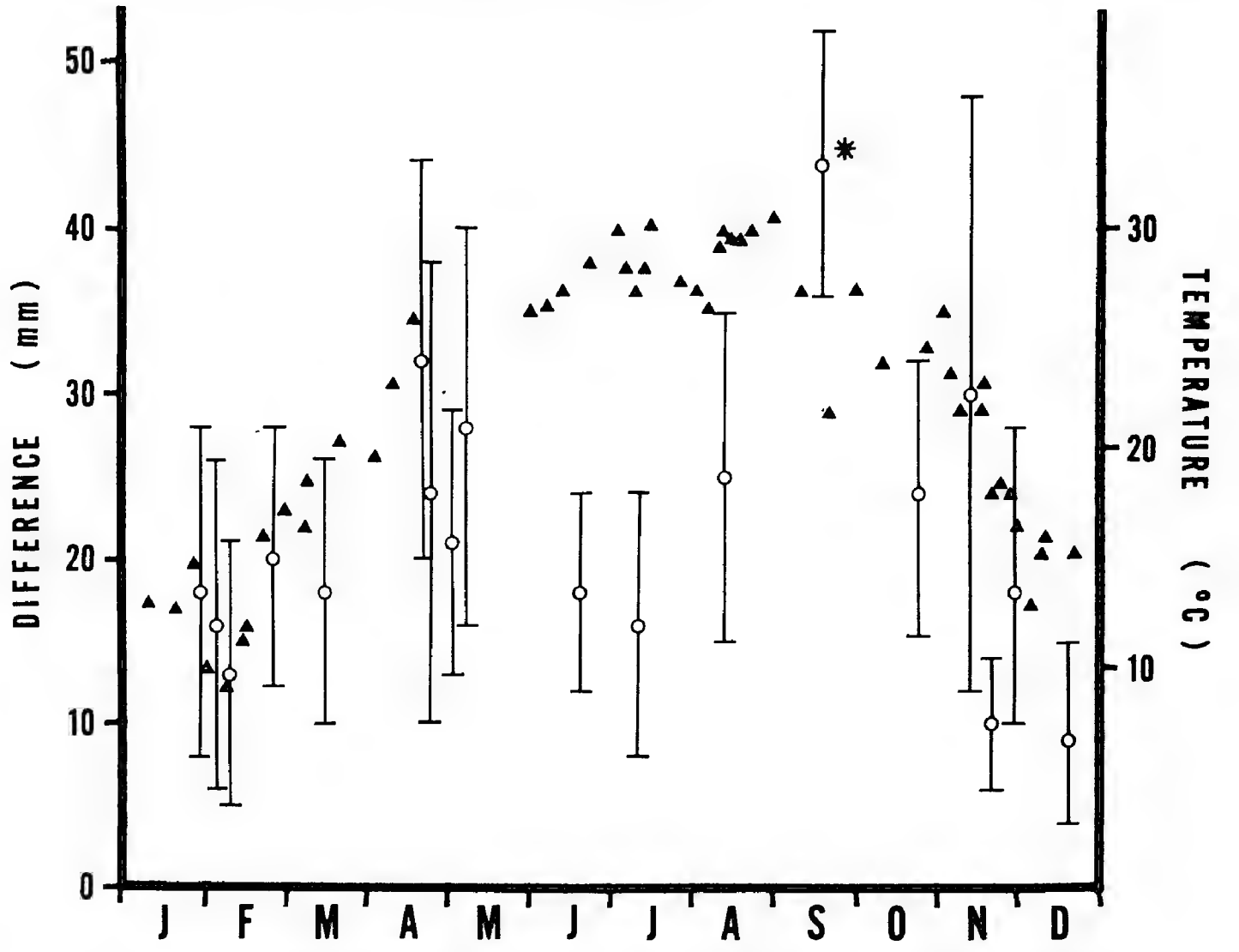

FIG. 1. Annual growth pattern of striped mullet in south Texas waters. Triangles denote sea water temperatures at Aransas Pass Inlet at Port Aransas, Texas and circles represent mean difference between the standard length of fish at capture and the last back-calculated standard length ± 2 standard errors. Asterisk refers to sample with 0 and I class fish only.

July–August increments and those for the small age 0 and I fish in September ($t = 4.98, P < 0.01$).

DISCUSSION

In general, the overall annual growth pattern of *Mugil cephalus* with late autumn to winter annulus formation is in accord with other studies of this species in the Gulf of Mexico (Broadhead 1958, Shireman 1965). The period of very slow growth or growth cessation and annulus formation corresponds well with the lowest seasonal temperatures (Fig. 1), following the spawning migration from coastal waters to the Gulf (Gunter 1945) and spawning (Arnold and Thompson 1958). As both immature and adult fish displayed annuli, the influence of late autumn to winter migration and spawning on time of annulus formation is probably relatively unimportant. Evidence for annulus formation at seasonally low winter temperatures has long been acceptable as cited by Lee (1920) and by later investigations for most temperate fishes.

When growth after annulus formation is plotted as in Fig. 1, most temperate species would have increments that follow reasonably well the approximate

sinusoid temperature curve with the greatest increments during the summer, as would be illustrated by data for the freshwater bluegill sunfish, *Lepomis macrochirus* (Gerking 1966), or for the Australian sea mullet, *Mugil dobula* (Thomson 1951). There is some evidence that more tropical populations of *Mugil cephalus* in Indian estuaries display a growth lag during June and July (Rangaswamy 1972). However, the summer growth decline for *M. cephalus* at Age I or older in south Texas is quite pronounced (Fig. 1) and is followed by a late summer and early autumn increase in growth rate. This seasonal growth pattern for the mullet corresponds to their seasonal respiratory metabolic pattern.

Field measurements of respiratory metabolism of *Mugil cephalus* in south Texas waters indicated that there was a pronounced depression in July and August, peaks at more moderate temperatures in spring and autumn, and a minimum in winter (Wohlschlag and Moore ms.). In this seasonal multiple regression study, respiratory metabolism was determined during the year both for brackish waters (12–24 ppt) and for coastal waters (30–35 ppt). During all seasons the fish swam approximately one body length sec^{-1}. By using regressions with seasonal average weights, swimming velocities and temperatures, comparable calculated brackish and marine routine oxygen consumption rates are in summary form in Table 3.

In laboratory data for slightly polluted open Galveston Bay, Texas waters as compared to "unpolluted" waters from Port Aransas, the summer respiratory metabolism for fasted mullet of both waters in July was only slightly above the spring and autumn levels (Wohlschlag 1973; Wohlschlag *et al.* ms.). However, other summer laboratory data for fasted mullet under carefully controlled temperatures did not reveal a respiratory depression, but these data were always for fish taken early in summer just as peak summer temperatures were reached and before a waning photoperiod.

Thus a straightforward ecological interpretation of the field experiments would be that growth rates (and presumably food intake) would have to decline, inasmuch as the mullet could not seemingly economize on energy expenditures by having either reduced maintenance or diminished swimming (foraging) requirements at prolonged high summer temperatures. Less parsimonious

TABLE 3

Comparisons of routine oxygen consumption rates in mg kg^{-1} hr^{-1} for *Mugil cephalus* in brackish and marine environments over four seasons and at average temperatures, weights and swimming velocities. Summarized from Wohlschlag and Moore (ms)

Season	Average Temperature °C	Mg O_2 kg^{-1} hr^{-1} Brackish	Marine
Summer	28.5	269	377
Autumn	20.6	453	560
Winter	15.5	316	363
Spring	22.9	561	586

interpretations of summer growth depressions could possibly involve statistical sampling anomalies, feeding impairments or changes in a variety of physiological or biochemical processes.

Statistically, except for the Age 0 and Age I classes in September (Fig. 1), there is no evidence to suggest that seasonal, differential growth increments were the result of selective sampling of age groups. Thus the data indicate that depressed summer *M. cephalus* growth rates followed high spring rates and preceded somewhat higher rates in autumn, when these increments were measured by the difference between the standard length at capture and the last back-calculated standard length from scale analyses of frequent collections during the year. Moore (1973) with a different series of *M. cephalus* scale data, from approximately the same south Texas area, but with somewhat smaller fish, obtained incremental growth results that also indicated a pronounced decrease of growth during sustained peak summer temperatures; summer growth checks occurred between August and October. As expected, the smallest growth increments are just before annulus formation and at the lowest seasonal temperatures. Statistically, the small incremental values of early winter (Fig. 1) would begin to appear when some of the fish possibly had begun to form the next annulus. Annulus formation as early as December might be possible for some early autumn spawners and yearling or older non-spawning mullet in the open coastal marine waters which usually would be around 20 C in December and not much lower than 17–18 C by January. Brackish open estuarine and bay mullet habitats, however, would have thermal regimes similar to that in Fig. 1, although much greater seasonal extremes are experienced in very shallow waters (Gunter 1945). Small increments could also appear from confusing summer false annuli with true winter annuli, but careful observations of individual scales permitted a rather clear assessment of winter growth cessation or diminution and annulus formation certainly by March.

Both statistically and physiologically, it is known that the older members of fish populations begin seasonal growth later, end seasonal growth sooner, and grow at slower rates than the younger members, although for this study too few fish were available for growth rate evaluation at each age. A detailed comparison of several populations with respect to age-growth differentials is given by Gerking (1966) for *Lepomis macrochirus*. A persual of the growth patterns of older fish in his study also reveals that some summer size levels drop below the seasonal curve drawn between spring and autumn size levels. Similar summer drops in growth rates appear to be indicated by many other growth studies. If these observations are not simply statistical vagaries and represent a fairly common phenomenon, they could, in part, explain the summer decline in the growth rates for summer *M. cephalus* in Fig. 1, which are derived from all ages from yearlings upward. Gerking (1966, 1971, 1972) has indicated that explanations for the size- or age-specific growth differentials depend on such physiological-ecological variables as effective length of growing season, food availability, feeding rates, food utilization rates, efficiency of food utilization and comprehensive metabolic requirements. In addition to these variables, less than optimal conditions of temperature, dissolved oxygen levels, salinity, light or photoperiod, and

general water quality would be expected to place a metabolic stress on fishes as indicated in the review by Fry (1971) who notes that stresses generally reduce the "scope" for activity. He suggests that scope, the difference between standard and active metabolism, is reduced because stresses either raise standard metabolism or reduce active metabolism, or both. Similarly, reduced scope would imply that the growth component of total metabolism may also be reduced. Wohlschlag and Moore (ms) note that scope for "routine" activity (swimming at about 1 body length/sec) is lowest in summer, moderate in winter, and highest in spring and autumn in both marine and brackish fish.

The summer metabolic and growth depressions for iliophagus *Mugil cephalus* occurs at a time when presumably food supplies of algal and detrital materials would be at a maximum. Data on benthic and attached algal fluctuations are unavailable. Standing crops of phytoplankton algae do on ocacsion decline in some of the local bays in the summer months (Holland, *et al.*, 1973, 1974), when the usual average temperatures are around 28 C and dissolved oxygen levels are above 5 ppm for most shallow coastal waters. While there is presently no evidence for food deprivation as a cause for summer growth depression of the *M. cephalus*, there is a likelihood that sustained high summer temperatures with somewhat reduced dissolved oxygen levels would be far below optimal for food assimilative efficiency (*e.g.*, Brett 1970a, b). From Fig. 1 and Table 3 the optimal temperature range for maximum growth and metabolism would appear to be about 20–25 C even though the thermal acclimatizational history of the individual fish used for growth analysis is unknown. Andrews and Stickney (1972) showed that there was an increased rate of weight gain from 18 to 30 C, but a decrease at 34 C, for the channel catfish, *Ictalurus punctatus*. While the mullet metabolism and growth rates at spring optima and summer minima might be directly related to feeding, the high metabolism in early autumn might also be related in part to energy requirements for gonadal maturation, for which data are unavailable, and to growth requirements. One other type of growth inhibiting situation could involve changes in quality of foods in summer from minor changes in species composition to an extreme change in dinoflagellate abundance and associated toxic materials in Gulf coastal waters (Gates and Wilson 1960), although no such extremes were observed before and during this study.

One of the best available explanations for growth and metabolic depression mechanisms at prolonged high temperatures, when high energy demands for maintenance and swimming would be required, involves a temperature-induced shift in biochemical pathways (Hochachka and Somero 1971). Somero (1973) indicated that such adjustments under high temperature, high activity, and low oxygen extremes caused an increase in the anaerobic glycolytic conversion of pyruvate to lactate in white muscle of *Gillichthys mirabilis*. Somero (pers. comm. to DEW) noted that a preliminary experiment with small *Mugil cephalus* showed little evidence of lactose dehydrogenase (LDH) activity and anaerobiosis to compensate for depression of aerobic metabolism. These and similar biochemical experiments suitably reinforce the observations of reduced growth and metabolism of the Gulf coastal *M. cephalus* (Wohlschlag and Moore ms.).

The depression of *Mugil cephalus* growth during prolonged high summer tem-

peratures has important implications in future management of fisheries or aquaculture for this and other similarly affected species. It should be noted here that preliminary, unpublished observations on both the pinfish, *Lagodon rhomboides*, and the spotted sea trout, *Cynoscion nebulosus*, have a high degree of false annulus formation in summer, which may indicate growth suppression. From Fig. 1 it is evident that if spring growth did not level off through the summer for the post-yearling individuals but continued to increase with the summer temperatures, there would be a considerably greater (perhaps 20–30%) increase in annual growth. Assuming that mortality rates are substantial during the summer, it is appropriate to set up exploitation models for harvesting fish at times that immediately follow maximal growth periods in order to maintain maximum sustainable yields (*e.g.*, Ricker 1958).

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THE POSSIBLE ORIGIN OF PECULIAR *THALASSIA TESTUDINUM* REPORTED FROM TEXAS AS *POSIDONIA OCEANICA*

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ABSTRACT

Peculiar plant fragments of *Thalassia testudinum* were erroneously reported from Texas as the Mediterranean *Posidonia oceanica*. These fragments may have originated from distant Caribbean or other Gulf of Mexico seagrass beds from which they were torn during a previous hurricane season. They probably owe their superficially somewhat *Posidonia*-like form to the long oceanic transport. When studied in laboratory cultures with *T. testudinum* transplanted from local Texas seagrass beds and *P. oceanica* from the Mediterranean coast of France, the Gulf fragments produced leaves that were wider than is typical of Texas plants but similar to those produced by *Thalassia* of more tropical origin in Mexico and Central America. The flavonoid composition of the beach fragments also was similar to that of *Thalassia*.

DISCUSSION

Posidonia oceanica (L.) Delile has been included as a possible seagrass of the Texas coast by Correll and Johnston (1970) and by Correll and Correll (1972). *Posidonia oceanica* is essentially a Mediterranean species (see den Hartog 1970). Prior to the reports from Texas, it had been reported outside of the Mediterranean only from the southernmost French Atlantic coast and from the Atlantic coasts of Spain, Portugal and Morocco (Wilkomm and Lange 1870; Daveau 1896; Rouy 1912; Jahandiez and Maire 1931; Pereira Coutinho 1939; Sampio 1947). In the Atlantic it extends only up to Biarritz to the north, and down to Tanger to the south of the Strait of Gibraltar (Jahandiez and Maire 1931). Douin (1932) remarked that this species is very rare on the Atlantic coast. Den Hartog in his recent monograph on the seagrasses of the world reports (1970, p. 126) that he has not seen any collections of *P. oceanica* originating outside the Mediterranean Sea. The identification of plants on Texas beaches as *P. oceanica* needed further investigation.

Four specimens identified by Correll as *P. oceanica* in the Lundell Herbarium of the University of Texas at Austin seem to be the basis of its inclusion in the Texas flora. These were collected in late April to mid-June of 1967 (J. R. Crutch-

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field 2521, 2942, 2951, 2991) on the Gulf beaches from the mouth of the Rio Grande to Galveston. Each of the four specimens was collected among beach debris that had been washed ashore from unknown sources.

Den Hartog (1970, pp. 34–45) presented a key for the identification of sterile material of seagrasses based on the works of a number of botanists who studied the morphology and anatomy of these plants (for references see den Hartog, *op. cit.*). The first step of the key separates plants with ligulate leaves from plants with non-ligulate leaves, hence, the marine Potamogetonaceae from the marine Hydrocharitaceae, respectively. The leaves of the Crutchfield specimens lack ligulae and these plants would be excluded from *P. oceanica*, a potamogetonacean species.

Correll and Johnston (1970) and Correll and Correll (1972) did not state which specimens from Texas were assigned by them to *P. oceanica*. Thus, the possibility remains that they had additional fragments, other than the Crutchfield specimens, which could belong to *P. oceanica*. However, the illustrations, a and b, of fig. 53 in Correll and Correll (1972) obviously represent the Texas beach fragments identified as *P. oceanica*. These illustrations completely agree with Crutchfield's specimens. The presence or absence of a ligula can not be checked on the illustrations, but both the illustrations and the specimens show short fibrous strands sparsely covering the rhizome. This latter property is typical for *T. testudinum* Banks ex König, indigenous to the Gulf of Mexico (see Correll and Correll 1972, g. 75a, b) but not for *P. oceanica*. The rhizomes of *Posidonia* are usually densely covered by much longer strands that when shed may leave the rhizome bare, but not sparsely covered with short strands (see Dory and Durieu 1850, pl. 25, fig. 8; Ostenfeld 1918, fig. 1; Weber 1956, fig. I,1).

Crutchfield's specimens were compared with *P. oceanica* from France (Mediterranean coast, leg. W. A. Hall and H. Wierner, no further details, UC 384322), Italy (Albissola Marina, W. Liguria, 7 and 12 October 1880, A. Piccone, fl., UC 1328292) and Cyprus (Cape Doles, 29 October 1968, E. Cohen, YL 5028), as well as with specimens of *T. testudinum* from the herbaria of the University of Texas at Austin and the University of California, Berkeley. Vegetative features of *P. oceanica*, *T. testudinum* and the Crutchfield specimens are compared in Table 1. The identification of Crutchfield's specimens as *P. oceanica* should be rejected on several bases: absence of ligula, strands on the rhizomes, root size and anatomy, rhizome size and shape, leaf blade tip morphology and anatomy (Table 1). However, the greater width of the leaves and the more robust condition of the Crutchfield specimens set them apart from local Texas populations of *T. testudinum*.

Peculiar *T. testudinum* plant fragments, very similar to Crutchfield's specimens, were found again on the Texas coast when we checked it for seagrasses in the spring of 1974. In April and continuously through May and into June, numerous fragments of the same seagrass form washed ashore on barrier islands on the central Texas coast from Port Aransas to Port Isabel intermingled with *Sargassum*, scattered seeds of *Rhizophora mangle* L., fruits of *Cocos nucifera* L. and seeds of *Mucuna urens* (L.) Medic. *Rhizophora*, *Cocos*, and *Mucuna* are not

Table 1. Some vegetative features of Posidonia oceanica, Thalassia testudinum, and the Crutchfield specimens from Texas[a]

	Posidonia oceanica	Thalassia testudinum	Peculiar Beach Fragments[b]
Rhizome	coarse, up to 1 cm in diameter	thinner, 3-6 mm thick	3-5 mm thick
	brown, blackening when dried	straw-colored, remains almost the same when dried	light straw-colored
	a sheath-like scale and a root at each node	a scale at each node, a root irregularly every 1-8 nodes	specimens have no scales, only one has roots at intervals of 1-many nodes
	scales usually about 2.5 cm long, when old completely torn, each into numerous closely situated bundles of fibrous strands, densely covering entire rhizome	scales usually 6-10 mm long, when old torn each into 6-9 spaced bundles of fibrous strands	short, 4-10 mm long spaced bundles of fibrous strands of the rhizome
Root	coarse, up to 4 mm thick	thin, ca. 1 mm in diameter	1 mm in diameter
	richly branched	usually unbranched or only once forked	unbranched
	texture dense in cross section	spongy in cross section, with wide longitudinal air channels	spongy in cross section, with wide longitudinal air channels
	undivided morphologically	septate at intervals of 1 mm	septate at intervals of 1 mm
Leaf Sheath	3-5 cm long, 10-12 mm wide	2-10 cm long	2-3 cm long
Ligula	short, up to 0.5 mm, inserted along the upward curved borderline between the sheath and the blade	absent altogether, transition between sheath and blade marked by a straight or a downward curved line	absent altogether, transition between sheath and blade marked by a downward curved line
Leaf Blade	40-50 cm long, 5-9 mm wide	10-60 cm long (including sheath), 4-15 mm wide (Texas: 4-7 mm; Veracruz, Mexico: 6-13; Belize, C. A. 9-15)	2-12 cm long, 6-10 mm wide
	regularly shed at the level of the ligula	irregularly torn from sheath when old	irregularly torn from sheath when old
	leaf-tip obtuse to emarginate, rarely tapering, often somewhat asymmetrical	leaf-tip rounded or obtuse, sometimes emarginate, usually symmetrical	leaf-tip rounded
	margin strictly entire, strengthened by fibrous sclerenchymatic fibers	margin very sparsely serrulate at the lower part of blade, densely serrulate at leaf-tip; in older leaves denticles often break, leaving only their colorless bases	margin very sparsely serrulate, densely so at the leaf tip
	nerves 13-17, connected by perpendicular cross-veins at intervals of 2-12 mm, median nerve usually a little more conspicuous than the other nerves	nerves 9-15, connected by perpendicular cross-veins at intervals of about 1-4 mm, median nerve usually much more conspicuous than other nerves	nerves 6-12, connected by perpendicular cross-veins at intervals of 3/4-1 1/2 mm, median vein more conspicuous than other veins
	texture dense in cross section, owing to the small air channels (see Sauvageau, 1890a, fig. 30), the diameter of which is usually about 1/10 of the leaf thickness, but may reach up to 1/3 the thickness	texture spongy in cross section, owing to the very wide air channels (see Sauvageau, 1890b, fig. 3), the diameter of which is often 2/3 of the leaf thickness	diameter of air channels up to 1/3 of leaf thickness
	outer walls of epidermis cells much thicker than other walls	outer walls of epidermis cells about the same thickness as other walls	outer walls of epidermis cells slightly thicker than other walls

[a] Main sources consulted for features of P. oceanica and T. testudinum were Sauvageau, 1890a, b, 1891, for anatomical and some morphological features, and den Hartog, 1970, for morphological features.

[b] Two of the collections by Crutchfield in 1967 were from Cameron County, Texas (no. 2951, Boca Chica Beach at the mouth of the Rio Grande; no. 2991 from Padre Island Beach across from Port Isabel). A third collection was from Nueces County (no. 2942, 5 miles south of Bob Hall Pier, Padre Island, east of Corpus Christi) and a fourth was from Galveston County (no. 2521, Stewart Beach on Galveston Island).

known as established populations on the Texas coast. Much of the material washed ashore in 1974 had a heavy coating of epibiota, including goose barnacles and fouling-type bryozoans. The 1967 collections also have attached goose barnacles, suggesting a possible long oceanic transport.

Several seagrass fragments freshly washed ashore in May were returned to the Austin laboratory and cultured for a year with plants of *Thalassia* and *Posidonia*. In synthetic seawater the beach fragments continued to produce short

leaves that were broader than those of the Texas *Thalassia* transplanted from Redfish Bay, near Port Aransas, but were morphologically distinct from those of *Posidonia* transplanted from Marseille, France. *Thalassia* plants from Veracruz, Mexico, that were cultured for six months in the laboratory also continued to produce wider leaves than those produced by transplants from Redfish Bay and from Lower Laguna Madre near Port Isabel, Texas.

Secondary compounds of *Thalassia* and *Posidonia* were compared with those of the beach fragments for further insight into their identification. The flavonoids were compared using methanol extracts of leaf tissue (0.5 g) and two-dimensional paper chromatography using the techniques of Mabry *et al.* (1970). Phenolic acids were compared in aqueous extracts of leaf tissue (5 g/100 ml HOH) following the methods outlined by Ibrahim and Towers (1960) using paper chromatography. A similar pattern of flavonoids was demonstrated (Table 2) in *Thalassia* collected in Redfish Bay(and in Lower Laguna Madre), Texas, in the fragments cultured in the laboratory and in fragments collected in 1967. *Posidonia* leaves collected in France and leaves cultivated in the laboratory lacked the flavonoids. The phenolic acids were similar in *Thalassia*, the beach fragments and in *Posidonia*.

The possibility of finding *Posidonia oceanica* outside the Mediterranean and washing ashore on Texas beaches was not likely but needed to be investigated. The specimens that washed ashore on the beaches of Mustang and Padre Islands in 1974, and possibly other years, are *Thalassia* fragments that may have been torn away from seagrass beds of the Caribbean or remote parts of the Gulf of

TABLE 2

Flavonoid patterns of *Thalassia testudinum*, *Posidonia oceanica*, and Texas beach fragments

Compound number[a]	Compound Characteristics: Rf values[b] B A W	HOAc	Fluorescence[c] $-NH_3$	$+NH_3$	Presence (+) or absence (—) of compounds: *Thalassia*[d]	*Posidonia*[e]	Beach fragments: Crutchfield 2951 (1967)[f]	Port Aransas (1974)[g]
1	.113	.214	d	d	+	—	+	+
2	.321	.375	d	by	+	—	+	+
3	.360	.389	d	d	+	—	+	+
4	.378	.119	d	yor	+	—	+	+
5	.470	.131	–	w	+	—	+	+
6	.575	.197	d	d	+	—	—	—
7	.760	.019	d	d	+	—	—	—
8	.857	.022	d	d	+	—	—	—
9	.630	.428	d	d	+	—	—	+
10	.605	.376	d	d	—	—	—	+

[a] Compounds 1–5 are tentatively assigned to flavone and flavonol, 7–0-monoglycosides and 7–0-diglycosides; 6 to flavonol 3–0-diglycosides and 3–0-monoglycosides; 7–8 to flavone and flavonol aglycones; 9–10 to dihydroflavonal aglycones (Mabry, Markham and Thomas 1970).

[b] Rf values recorded on Whatman no. 1 paper in the solvent systems: BAW, t-butyl alcohol, HOAc, HOH (3:1:1); HOAc, 15%.

[c] Fluorescence under UV, 365 nm. Colors: d, dark absorbing; by, bright yellow; yor, yellow orange; w, white.

[d] *Thalassia* leaves collected in Redfish Bay, near Port Aransas, Texas.

[e] *Posidonia* leaves collected at Marseilles and Le Bruse, France by Dr. M. Ledoyer.

[f] Crutchfield specimen collected at Boca Chica Beach at the mouth of the Rio Grande.

[g] 1974 beach fragment collected on Mustang Island beach at Port Aransas, Texas. Leaves from plants collected at Veracruz, Ver., Mexico, in 1974, also lacked compounds 6, 7, and 8.

Mexico during tropical storms. *Thalassia* specimens that were collected and cultured in the present study from Arrecife Hornos in Veracruz, Ver., Mexico and from San Pedro Island, near Belize City, Belize, C. A., represent a robust form that is similar to the type which washes ashore on the Texas beaches.

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ADDENDUM

Peculiar *T. testudinum* plant fragments were found again on the beaches of the barrier islands of Texas in 1975. The fragments again washed ashore intermingled with *Sargassum* from April through June and into early July. Some of the fragments collected in late June had the largest rhizomes that have been reported for *T. testudinum*, 8–10 mm in diameter.

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DAY DEGREE GROWTH MODELS FOR INTERTIDAL OYSTERS

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ABSTRACT

Linear and polynomial day degree models are shown to be capable of predicting oyster growth in terms of height or weight. Polynomial models predict growth more accurately than linear models, but are less meaningful biologically. A general linear model for predicting oyster growth in terms of weight is developed for the North Inlet, South Carolina area.

INTRODUCTION

The utilization of mathematical methods to describe the growth of oysters is essential to the development of productivity estimates of estuarine ecosystems. It is well known that growth in oysters and other bivalves is influenced by temperature (Butler 1953; Taylor 1959, 1960). The utilization of day degrees as a measure of heat energy to describe the growth or development of many kinds of organisms is an established practice (Allee *et al.* 1949; Krogh 1914). Boetius (1962) has shown that day degrees (the mean temperature at a time period multiplied by the number of days in the period) and growth are linearly related as follows:

$$W = a + b\,Q \qquad (1)$$

where W is a measure of size, Q is the number of day degrees and a and b are the linear regression coefficients. The concept of day degrees in relation to growth has been incorporated into the von Bertalanffy growth equations by Ursin (1963). The utilization of the linear day degree model to describe the growth of oysters is advantageous for two reasons: (1) traditional growth models usually require an exact age estimate of the organism, but such estimates are extremely difficult to obtain for oysters from natural populations; and (2) growth is influenced by environmental parameters and temperature is an important variable in the estuarine environment.

METHODS

The growth of intertidal oysters was observed in Clambank Creek, part of the North Inlet estuarine ecosystem near Georgetown, South Carolina. Growth observations were made during two different years. For the first group, intertidal oysters of different sizes were collected from Clambank area, separated into individuals, scrubbed to remove fouling organisms and the shells numbered with permanent black ink. The oysters were dried and weighed to the nearest 0.01g. Between observations the oysters were kept in a wire cage suspended in the intertidal zone at

Clambank. The oysters were weighed 13 times between February, 1970 and January, 1971. The time interval between weighings varied from 21 to 49 days. At each weighing the oysters were scrubbed and the old numbers retouched. In this group, only growth data from oysters which survived the entire year was used.

In the second group, the growth of the intertidal oysters was observed from May 10, 1972 to October 28, 1972 with interim measurements on June 23 and July 18. In this series of observations, four size groups were established according to shell height in milimeters. The size groups were 20–49mm, 50–74mm, 75–99mm and larger than 100mm. Shell weight was measured using a vernier caliper and the oysters were kept in wire cages which lay on the substrate in the intertidal zone.

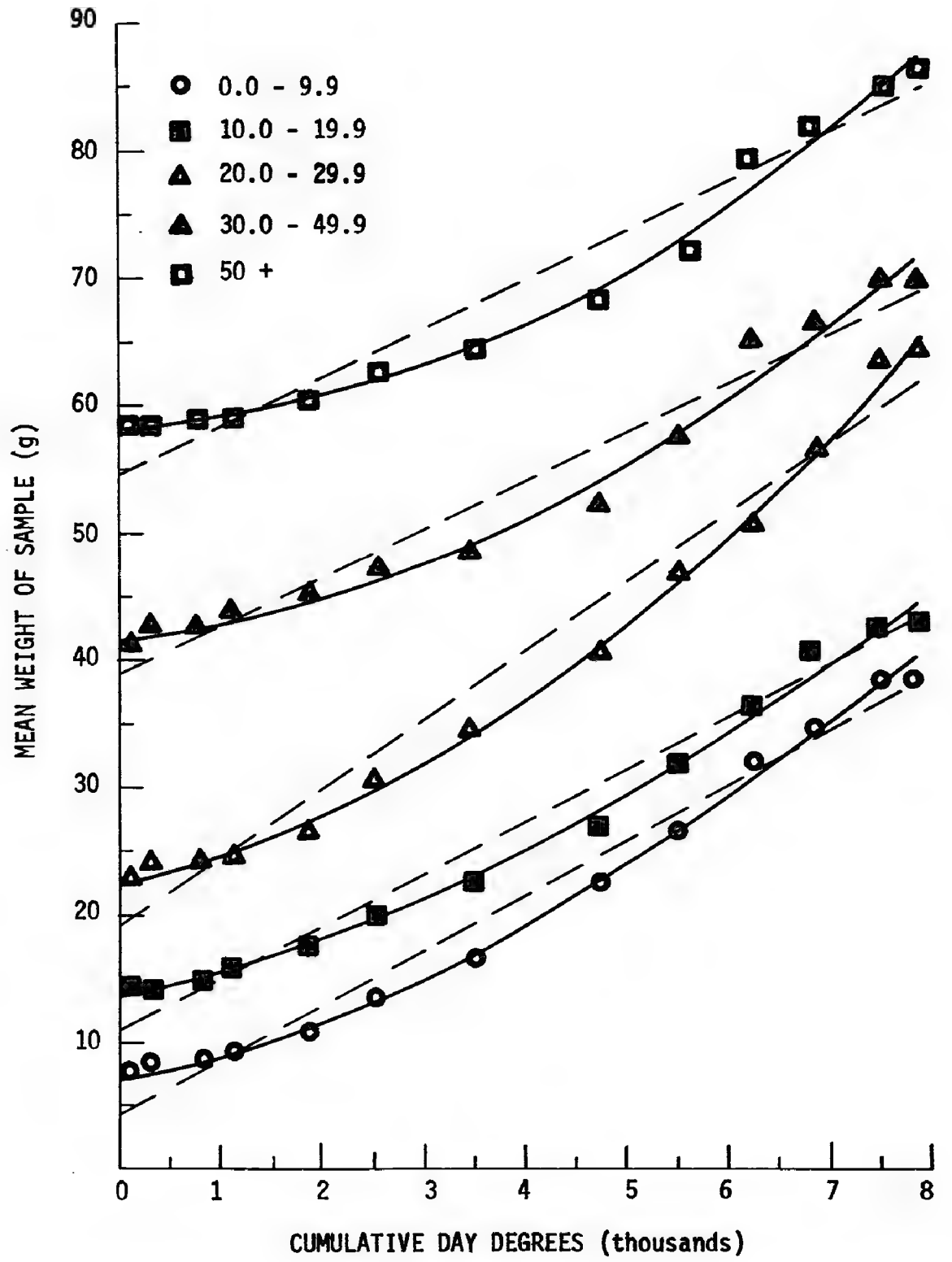

FIG. 1. A comparison of the linear models (dashed lines) and quadratic models (solid lines) for growth in whole weight of different size groups plotted against cumulative day degrees.

TABLE 1

Linear and quadratic equations describing the relationship between mean sample weight and day degrees; n denotes the number of organisms observed for each mean and r^2 is the coefficient of determination

Initial Group Size	Equations	r^2	n
0.0 — 9.9	$W = 4.55 + 0.0040Q$	0.96	4
	$W = 6.99 + 0.0017Q + 0.00000032Q^2$	0.99	4
10.0 — 19.9	$W = 11.28 + 0.0040Q$	0.96	15
	$W = 13.40 + 0.0018Q + 0.00000028Q^2$	0.99	15
20.0 — 29.9	$W = 19.46 + 0.0053Q$	0.95	7
	$W = 23.67 + 0.0011Q + 0.00000055Q^2$	0.99	7
30.0 — 49.9	$W = 38.91 + 0.0038Q$	0.95	7
	$W = 41.64 + 0.0010Q + 0.00000036Q^2$	0.98	7
50.0 +	$W = 54.91 + 0.0038Q$	0.94	5
	$W = 58.28 + 0.0035Q + 0.00000044Q^2$	0.99	5

RESULTS

The seasonal variation in water temperature at Clambank is described by Equation 2 (Dame 1972):

$$T = 20.91 + 9.97 \sin D \qquad (2)$$

where T is temperature in C and D is the time in angular degrees (day one is February 7). Equation 2 was used to compute by integration the mean temperature between weight observations, which in turn was used to calculate the day degrees between observations.

The seasonal mean whole weight of different size groups in the first series of observations plotted against day degrees is shown in Figure 1. The mean whole weight values were used instead of all the data points. The linear models are depicted by dashed lines but do not explain the cyclic fluctuations in the data. The solid curves represent quadratic equations fitted to the same data and show a closer fit. Table 1 gives the linear and quadratic equations which best fit the

TABLE 2

Linear and quadratic equations describing the relationship between mean sample height in millimeters and day degrees; n denotes the number of organisms observed for each mean and r^2 is the coefficient of determination

Initial Group Size (mm)	Equations	r^2	n
25 — 49	$H = 40.64 + 0.0033Q$	0.88	95
	$H = 37.94 + 0.0079Q - 0.00000089Q^2$	0.99	95
50 — 74	$H = 62.86 + 0.0020Q$	0.81	205
	$H = 61.05 + 0.0051Q - 0.00000060Q^2$	0.94	205
75 — 99	$H = 85.12 + 0.0005Q$	0.93	127
	$H = 84.86 + 0.0010Q - 0.00000009Q^2$	0.98	127
100 +	$H = 105.94 + 0.0009Q$	0.82	32
	$H = 105.32 + 0.0020Q - 0.00000020Q^2$	0.90	32

data in Figure 1. The r^2 value or coefficient of determination gives an estimate of how well the fitted equations explain the variations in the data.

The mean shell height of the four size groups used in the second series of observations are plotted against day degrees in Figure 2. The linear equations which describe these observations are given in Table 2.

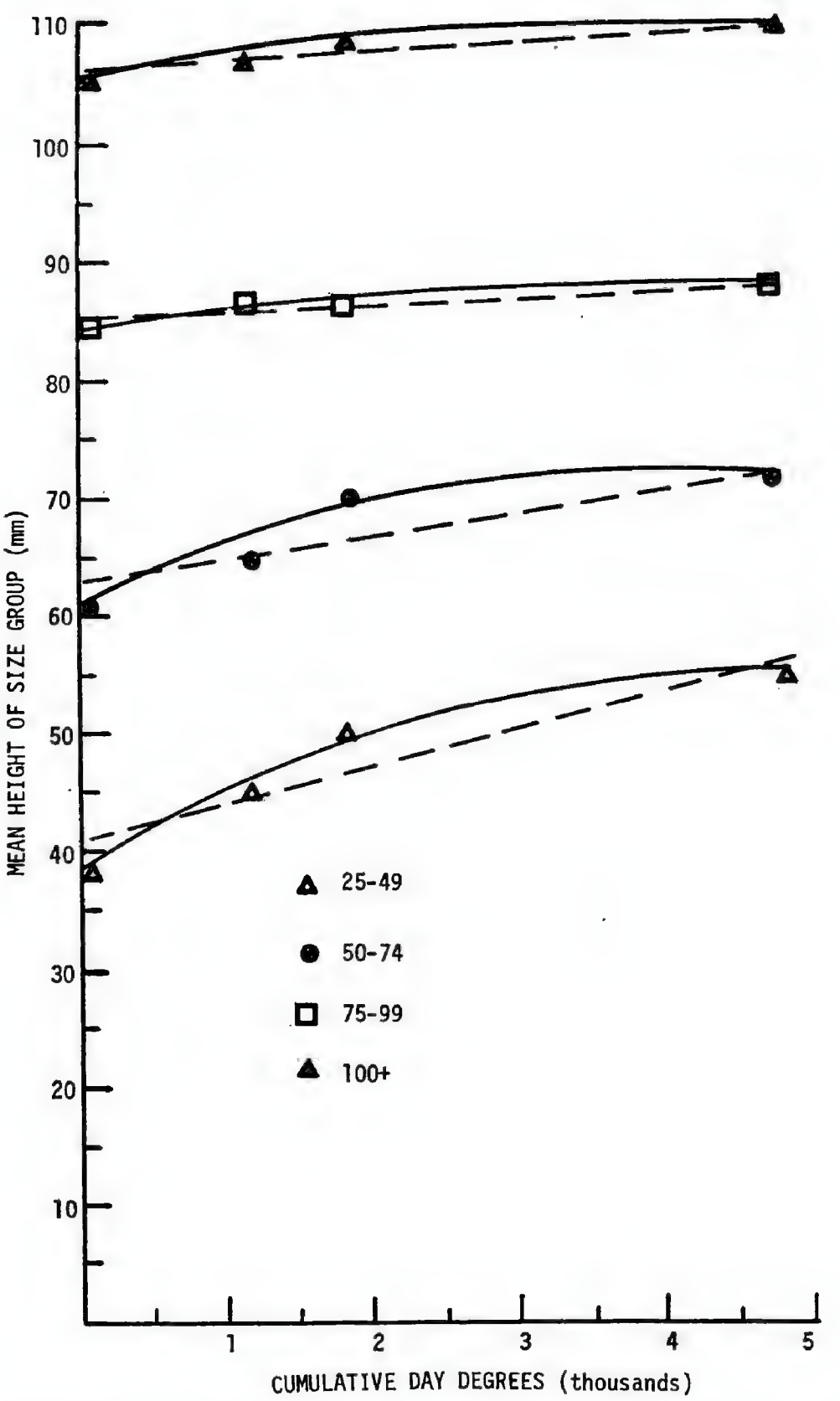

FIG. 2. A comparison of the linear models (dashed lines) and quadratic models (solid lines) for growth in height of different size groups plotted against cumulative day degrees.

DISCUSSION

The linear day degree models utilizing whole weight observations explain at least 94% of the variability in the seasonal growth of intertidal oysters, but fail to accurately describe all the fluctuations in growth rate. In the linear day degree weight models, the slopes (coefficient b) show some variation with size and the Y-axis intercepts (coefficient a) represent the initial weight of the oysters. If the slopes of the linear weight models are assumed to remain constant with size a general linear day degree weight model for intertidal oysters in the North Inlet area can be constructed with the following form:

$$W_{t+1} = W_t + 0.004\,\Delta Q. \tag{3}$$

W_t is the initial weight, W_{t+1} is the weight at the end of some time period and ΔQ is day degrees in that time period.

The growth data from the second series of observations utilizing shell height measurements does not fit either the linear nor the quadratic day degree models as well as the whole weight observations. It was not possible to develop a generalized linear day degree height model similar to Equation 3 because the slope of the height models varied a great deal. The shell height method could be more easily used by the commercial oysterman in measuring growth rates and predicting harvest times because this method requires less work.

The quadratic day degree models do offer an increase in the accuracy of prediction for the observed data, but would give completely erroneous predictions of growth if extended to future years without new data. In addition, the coefficients of the quadratic or polynomial models have not as yet been shown to have any biological meaning (Mead 1971).

The most prominent growth models in marine biology are the Gompertz (Silliman 1966), the Kruger (Kruger 1965), the Taylor (Taylor 1962) and the von Bertalanffy (von Bertalanffy 1957). The von Bertalanffy model has been related to temperature in describing the growth of several bivalves (Taylor 1959, 1960; Ursin 1963). Although the physiological principles upon which the von Bertalanffy models are based have been questioned by Ricker (1958), Richards (1959) and Hemmingsen (1960), there is still a need to adequately predict the growth of organisms in relation to temperature. It is also possible that by fitting data to emperical formulae with little or no theoretical background new relationships and theory may be found (Paloheimo and Dickie 1965). This study offers a relatively easy method of predicting growth in oysters utilizing a general linear day degree model applicable to organisms in similar habitats and a more specific group of non-linear day degree models which might be used for more accurate growth predictions.

ACKNOWLEDGMENTS

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A NOTE ON STANDING CROPS OF *SPARTINA ALTERNIFLORA* IN TEXAS AND FLORIDA

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ABSTRACT

A late summer survey of eight *Spartina alterniflora* marshes in Texas and Florida was conducted. The live biomass is equivalent to or slightly greater than that found on the north Atlantic coast, but the dead biomass is considerably greater. Grass height: biomass relationships previously described for North Carolina and Rhode Island marshes are valid for the Gulf marshes. The slopes of the regression equations appear to increase with decreasing latitude and reflect changes in stem density and weight.

INTRODUCTION

Salt marshes dominated by *Spartina alterniflora*, Loisel. have received a great deal of attention on the eastern U.S. coast, yet little attention has been given to them on the Gulf of Mexico coast. Kirby (1972) documented productivity of streamside and inland *S. alterniflora* in a Louisiana coastal marsh, but in her review of marsh production, Keefe (1972) mentions no data from Texas or Florida. This lack of information exists despite the known dependence of most commercial species of fish on marsh-estuarine areas and in spite of the fact that the Gulf Coast has an estimated 63 percent of the nation's coastal wetlands (Table 1). *Spartina alterniflora* is an important component of these wetlands, and this report discusses a late summer survey of *S. alterniflora* standing crops in this area. All seasonal studies on *S. alterniflora* have shown that live standing crop is near maximum at this time. Such measurements do not accurately measure the total production of the plant since leaf abscissions, death of plants before harvest, and grazing losses are not included (Williams and Murdoch 1969; Smalley 1958; Kirby 1972). However, annual organic production and nutrient inputs into the estuary by the plant are at least partially related to the amount of standing crop (Pomeroy *et al.* 1968; Reimond 1972; Turner 1974) and such measurements are useful as a relative index of macrophyte productivity.

METHODS

A field survey was conducted from Brownsville, Texas, to Tampa, Florida, on August 19 to 26, 1974. Potential locations allowing easy access to wetlands were selected from previous surveys of Texas, Alabama, Mississippi and Florida coastlines (James *et al.* 1972; Christmas 1973; Crance 1971; and McNulty *et al.* 1972, respectively). Because of inclement weather, time constraints and difficuly in locating large monotypic stands of *S. alterniflora* (>100 m^2), only eight sites were examined fully enough to be included in these results. Despite two days of effort, no

TABLE 1

Area of Coastal Marshes in the United States[1]

Area[1]	ha × 10^3	Percent of Total	Source
Atlantic Coastal States (including E. Florida)	942.3	36	Spinner 1969
Florida—W. Coast			
Tidal Marsh	214.0	8	McNulty *et al.* 1972
Mangrove	159.2	6	McNulty *et al.* 1972
Alabama	4.8	< 1	Crance 1971
Mississippi	27.1	1	Christmas 1973
Louisiana	1062.9	41	Chabreck 1972
Texas	161.1	6	James *et al.* 1972
West Coast (California, Oregon, Washington)	30.8	1	Macdonald & Barbour 1974
Total	2602.2	99	
Gulf Area	1629.1	63	

[1] Water surface area excluded.

suitable sites were found south of Corpus Christi, Texas. In south Florida much of the intertidal area is dominated by *Juncus* spp. with *S. alterniflora* usually confined to narrow 10 m wide bands along creeks. The eight sites chosen were as follows (see Figure 1):

1. Corpus Christi, Texas, along Rt. 181 near Portland, Texas. A 1 ha site on a clay substrate mixed with organic matter.
2. Bayside, Texas, along Rt. 136. A 40 m diameter, thick, stand on a clay substrate.
3. Aransas National Refuge, Texas, along Big Tree Trail. A stand 500 m long, 40 m wide on clayey substrate.
4. Near Sabine Pass, Texas (16 km south) on Texas Rt. 87. A stand approximately 100 m wide and several km long.
5. St. Joseph State Park, Florida, Rt. 30E. North side of the peninsula, approximately 100 m in diameter on organic/clay substrate.
6. On Rt. 98, 16 km west of Carrabel, Florida, near Yent Bayou, 100 m in diameter bordered by *Juncus* spp.
7. Panacea, Florida, on Rt. 373, approximately 2000 m^2.
8. Dekle Beach, Florida, near the Fenoway River and Rt. 361, approximately 2 ha on a very peaty substrate.

All the stands appeared uniform in density and height. Plant height was measured at a minimum of 25 locations within each site to determine the average height for the whole marsh. At each site at least five 0.25 m^2 samples were harvested. The plants were separated into mature, young (< 0.5 m), and dead parts. The length of individual stems was measured and a mean length determined for the sample. The vegetation was stored at room temperature until it was dried at 65 C for 2 days, and then weighed. From the regression equation: log (biomass) = $a_0 + a_1$ (height), the average standing crop of live material for the whole marsh was calculated separately for the Texas and Florida marshes.

RESULTS AND DISCUSSION

Table 2 shows the predicted biomass of live *Spartina alterniflora* biomass at the eight sites sampled, average weight of individual mature, young, and dead stems, and the live:dead ratio. The late summer biomass of live material seems compar-

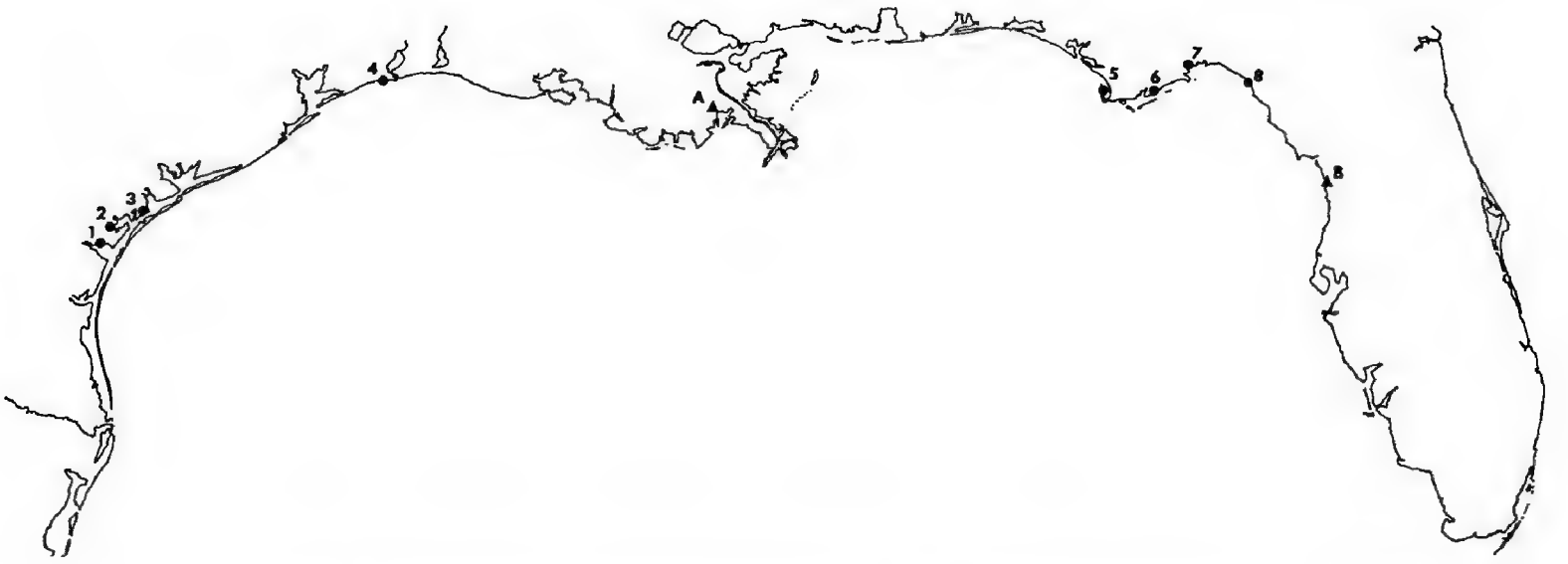

FIG. 1. Sampling location for *Spartina alterniflora* on the Gulf coast (sites 1–8, this study; site A, Kirby 1972; site B, Young 1974).

able to that on the east coast or slightly higher (compare Keefe 1972) but it appears to decrease at the extremes of its range (sites 1, 8, and B).

Compared to Atlantic marshes there is a great deal of dead material present in August. Kirby (1972) and Young (1974) have shown this to be true all year. In Georgia (Smalley 1958), North Carolina (Williams and Murdoch 1969) and Connecticut (Steever 1972) the amount of dead material present is seasonal and in August, relative to the live material, is very low.

In light of these data the persistent argument that tidal amplitude itself strongly influences productivity of the whole marsh in a positive manner seems

TABLE 2

Gram Dry Weight of Mature, Young and Dead Stems and the Predicted End-of-the-year Standing Crop at Several Locations in the Gulf of Mexico

Location (Fig. 1)	Latitude	Stem Weight (±std. dev.) Mature	Young	Dead	Live/Dead Ratio	Predicted[1] Biomass m^{-2} Mature	Total Live	Source
1	27.10	16.7± 8.8	3.2± .76	8.2±4.0	1.9:1	361	382	This study
2	28.10±	28.8±14.8	4.7± .92	14.4±9.0	1.2:1	798	938	This study
3	28.20	13.4±11.6	3.9± .81	10.1±2.0	1.8:1	406	735	This study
4	29.20	33.0± 8.3	4.0±1.4	17.6±8.4	1.0:1	744	923	This study
5	29.50	12.4± 5.3	3.4± .65	15.6±4.3	1.8:1	545	772	This study
6	29.55	.....	.....	.....	....	410	593	This study
7	30.10	23.1± 2.3	1.7± .7	18.1±1.7	1.8:1	585	824	This study
8	29.5	.....	.....	.....	....	428	617	This study
Ave.	...	21.2	3.5	14.0	1.6:1	559	769	This study
A. Barataria Bay, La.	29.3	.....	.....	.....	1.1:1	...	845 (Marsh avg.)	Kirby 1972
B. Crystal R. Florida	28.55	.....	.....	.....	1.7:1	...	580	Young 1974

[1] Predicted from the equations in Figure 2 and the average height of plants determined for each marsh.

too simplistic. The mean (but irregular) diurnal tidal amplitude at these Gulf Coast sites averages less than 30 cm. This is considerably less than Georgia's salt marshes (approx. 250 cm, semi-diurnal) which have a similar standing crop (Smalley 1958). The tidal energy is probably influential, however, in physically fragmenting dead vegetation, and the low energy regime of the Gulf Coast would

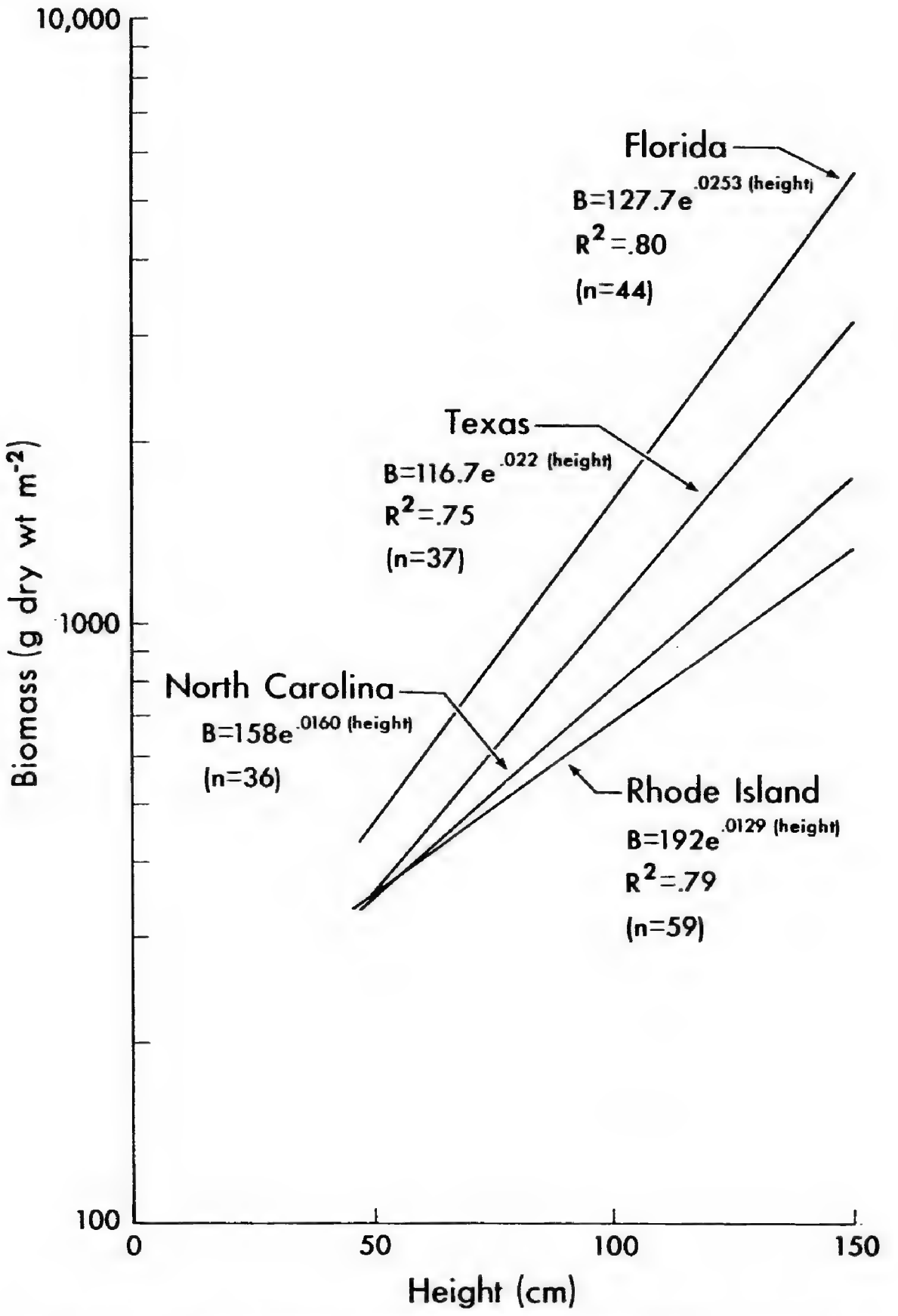

FIG. 2. Regression models for Rhode Island (Nixon and Oviatt 1973), North Carolina (Williams and Murdoch 1969), and Florida and Texas (this study). B = biomass; R^2 = coefficient of determination; n = samples used to derive the regression model.

TABLE 3

Stem Characteristics at Four Locations (dry weight of live culms)

Location	g/stem	g/cm stem	Source
Connecticut	2.99	.072	Turner, unpublished data
North Carolina	8.26	.0633	Marshall 1970
Texas	22.97	.272	This Study
Florida	17.75	.245	This Study

partially explain the greater proportion of dead material in these marshes relative to Georgia.

It is interesting to note that the weight of dead culms is only 50–75 percent of the weight of mature live culms. This means that 25–50 percent of the live organic weight is lost just before or soon after death, either by translocation to the roots, by leaching, or by decomposition of the above ground material.

Williams and Murdoch (1969) and Nixon and Oviatt (1973) developed equations relating average stand height to biomass in North Carolina and Rhode Island marshes, respectively. Their equations are shown in Figure 2 with similar equations calculated separately for our Florida and Texas data. The model fits our data about as well as it fit the Rhode Island data ($R^2 = 0.8$), but the slopes of the regression equations are different. There appears to be a consistent increase in the slope with decreasing latitude. That is, along the Gulf Coast, compared to the North Atlantic coast, biomass increases more for equal increments of height. The differences are attributable to variations in weight of individual culms and in stem density at different sites (Table 3). For instance Marshall (1970) observed stem densities of over 1000/m² in North Carolina, and in Connecticut they may be equally as dense (Turner, unpub. data). The Gulf Coast sites, in comparison, had 100–200 stems/m² which is consistent with Young's (1974) observations in Florida. Also, the Gulf Coast culms are heavier per unit length.

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DIEL FLUCTUATIONS IN CATCHES OF JUVENILE BROWN AND WHITE SHRIMP IN A TEXAS ESTUARINE CANAL[1]

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ABSTRACTS

A 2.7-ha portion of a canal near Texas City, Texas, was trawled over a 48-hour period to measure diel fluctuations in catches of juvenile brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*) and to evaluate the relative influence of selected environmental variables on such fluctuations. No significant day *vs.* night differences were detected in catches of brown shrimp, but catches of white shrimp were significantly ($P < 0.01$) higher during daytime. Observed correlations between catch and tide elevation and temperature were believed to be coincidental.

INTRODUCTION

The continued expansion of the shrimp fishery of the Gulf of Mexico has stimulated renewed interest in the dynamics of exploited populations of juvenile shrimp in estuarine areas. Analytical methods combining fishing-success and mark-recapture data are being evaluated as a means of estimating rates of fishing and natural mortality in these populations (Clark and Caillouet 1973). Because such studies involve sequential sampling the possibility exists for bias from diel changes in activity of shrimp. This study was conducted to measure diel fluctuations in catches of juvenile brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*) so as to provide the necessary baseline data for use in scheduling sampling work in studies of this nature.

Diel activity patterns of adult brown and white shrimp are well documented. Adult brown shrimp are nocturnal and burrow by day (Hughes 1969), but adult white shrimp are diurnally active and are thought to burrow at night (Idyll 1950). Diel fluctuations in catches of postlarval shrimp also have been studied. Baxter (1964) and Williams and Deubler (1968) found catches of postlarval brown shrimp to be higher at night than during daytime in Texas and in North Carolina, respectively; and Caillouet, Fontenot and Dugas (1968) obtained similar results for white shrimp in Louisiana. However, St. Amant, Broom and Ford (1966) and Caillouet, Perret and Dugas (1970) were unable to show any relationship between catches of postlarval brown shrimp and time of day in Louisiana waters. In the case of juveniles, Joyce (1965) observed high catches of

[1] Contribution No. 389, National Marine Fisheries Service, Gulf Coastal Fisheries Center, Galveston Laboratory, Galveston, Texas 77550. MARMAP Contribution No. 27.

juvenile brown shrimp during daylight hours in northeast Florida, and Trent (1967) reported both diurnal and nocturnal emigration, although the shrimp were observed to travel nearer the bottom during daylight hours. However, King (1971) reported that emigration in juveniles of this species occurred exclusively at night. Pullen and Trent (1969) sampled emigrating juvenile white shrimp during daylight hours and observed a similar pattern of movement.

The effects of other environmental variables on diel activity patterns also have been considered. General agreement exists that catches of brown and white shrimp postlarvae are higher at flood tide than at other tidal stages (Copeland and Truitt 1966; St. Amant *et al.* 1966; Caillouet *et al.* 1968), although Caillouet *et al* (1970) observed peak catches of postlarval brown shrimp on both high and low tides. Emigrating juvenile brown shrimp have been reported to move only on ebb tides (King 1971). Temperature and salinity changes may also influence diel activity patterns. Aldrich, Wood and Baxter (1968) observed pronounced activity changes in postlarval brown shrimp in response to slight variation in temperature. However, King (1971) found no correlation between catches of emigrating juvenile brown shrimp and changes in temperature or salinity.

STUDY AREA AND METHODS

The study was conducted in a 2.7-ha portion of a man-made canal opening into Dollar Bay near Texas City, Texas (Fig. 1). The portion sampled is approximately 915 m long and averages 30 m in width. The bottom consists of mixed mud and shell. Average depth is approximately 1.5 m. The canal is bordered by earthen-fill levees surrounded by broad expanses of tidal marsh. During the study, salinities in this area were low (under 10‰), turbidity was high, and tidal amplitude approximated 20 cm.

During a 48-hour period (July 6–8, 1973) 96 sequential 5-minute tows were made in the canal at half-hour intervals with a 3-m otter trawl (2.5-cm stretched mesh). Consecutive tows were made in opposite directions to compensate for possible effects of changes in speed and direction of tidal current. Prior to each tow, tide elevation[2] was recorded and water temperature was measured to the nearest C. Salinity was measured to the nearest part per thousand at 8-hour intervals. Following each tow, the shrimp caught were identified to species, counted and total length (tip of rostrum to tip of telson) was measured to the nearest millimeter. In tows in which the number of individuals of either species exceeded 50, subsamples of 50 individuals of that species were measured; otherwise, all individuals were measured.

RESULTS AND DISCUSSION

Catches of brown and white shrimp, and tide elevation and water temperature, are plotted against Central Standard Time in Figure 2. The cross-hatched area indicates "night," which includes the period from one-half hour after sunset to one-half hour before sunrise. For all catches combined, the mode in total length of brown shrimp was 90 mm (range, 46–114 mm); the mode for white shrimp was 60 mm (range, 35–97 mm). Brown shrimp catches exhibited no obvious diel cycle, but white shrimp catches were lower during the hours of darkness than

[2] This refers only to measured changes during the study, and it does not apply to absolute heights above or below some standard such as mean sea level.

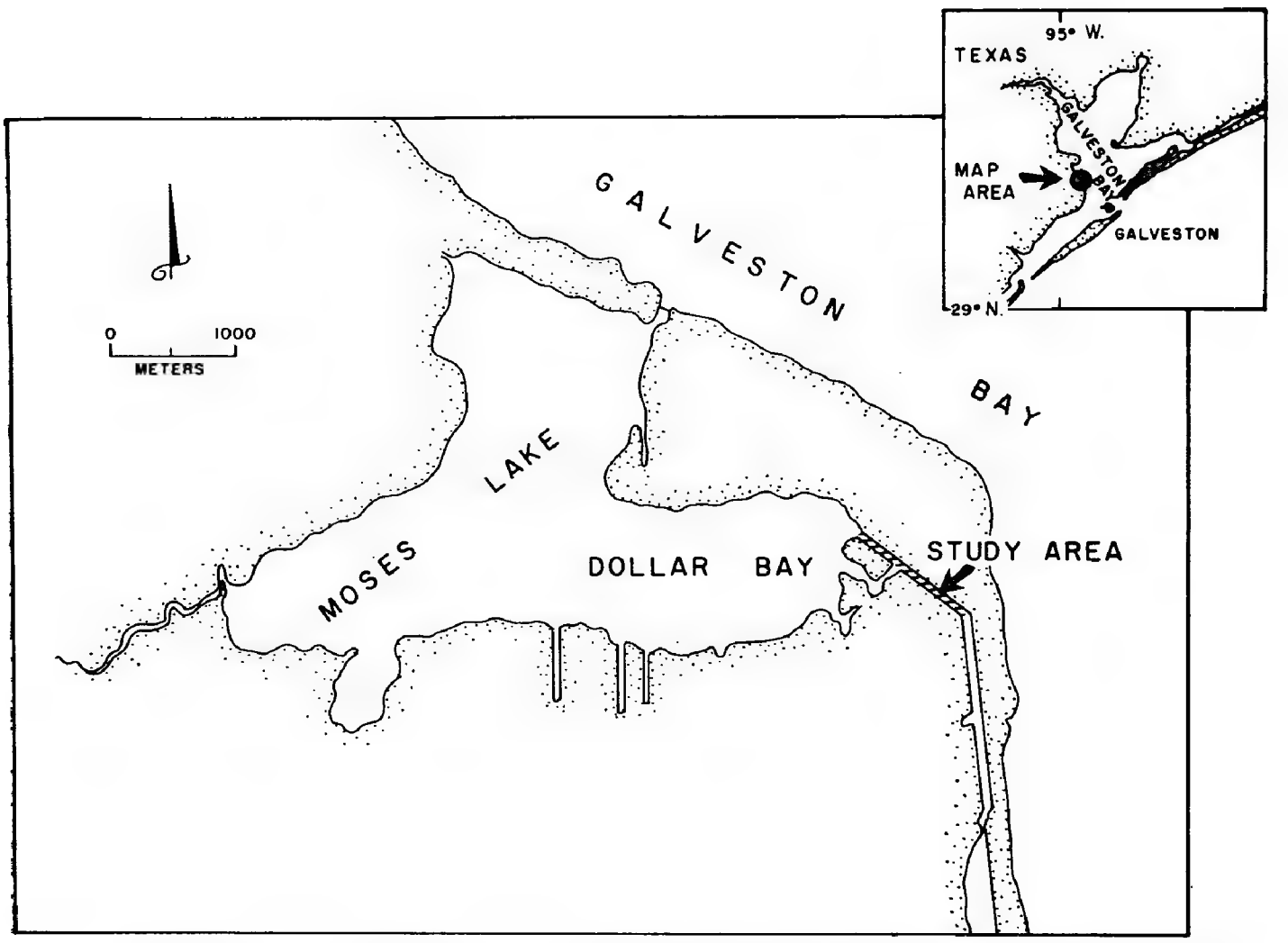

FIG. 1. Map of Dollar Bay and vicinity, Texas City, Texas, giving location of the study area.

during daytime (Fig. 2). Analysis of variance[3] revealed no significant day-to-day or light *vs.* darkness (day *vs.* night) differences in brown shrimp catch (Table 1), but a significant ($P < 0.01$) difference occurred between daytime and night catches of white shrimp (Table 2).

Our results for brown shrimp are similar to those reported by Joyce (1965) and by Trent (1967) and suggest a tendency for diurnal activity under turbid (or cloudy) conditions; King's (1971) study indicates that a closer relationship may exist between diel activity patterns and the light-dark cycle where water is clearer. Similarly, Eldred, Ingle, Woodburn, Hutton and Jones (1961) reported diurnal activity in juvenile pink shrimp (*Penaeus duorarum*), although pronounced activity changes in response to the light-dark cycle also have been documented in the field (Fuss 1964) and under laboratory conditions (Fuss and Ogren 1966; Hughes 1969). Hughes (1969) was able to demonstrate a circadian rhythm of pink shrimp activity in phase with the light-dark cycle; further, he observed an extremely close relationship between emergence from the substrate and the timing of the light-dark transition. It is possible that a similar rhythm exists in juvenile brown shrimp which is subject to modification under turbid or cloudy conditions.

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[3] Because the number of tows differed between daytime and night, a method for proportional subclass numbers was used.

The possible influences of salinity, tide and temperature remain to be considered. Salinity remained approximately 9‰ throughout the study and had no apparent influence on catch of either species. However, a significant ($P < 0.01$) negative correlation ($r = -0.35$) was observed between transformed catches (see Table 1) of brown shrimp and tide elevation, suggesting that tide may have

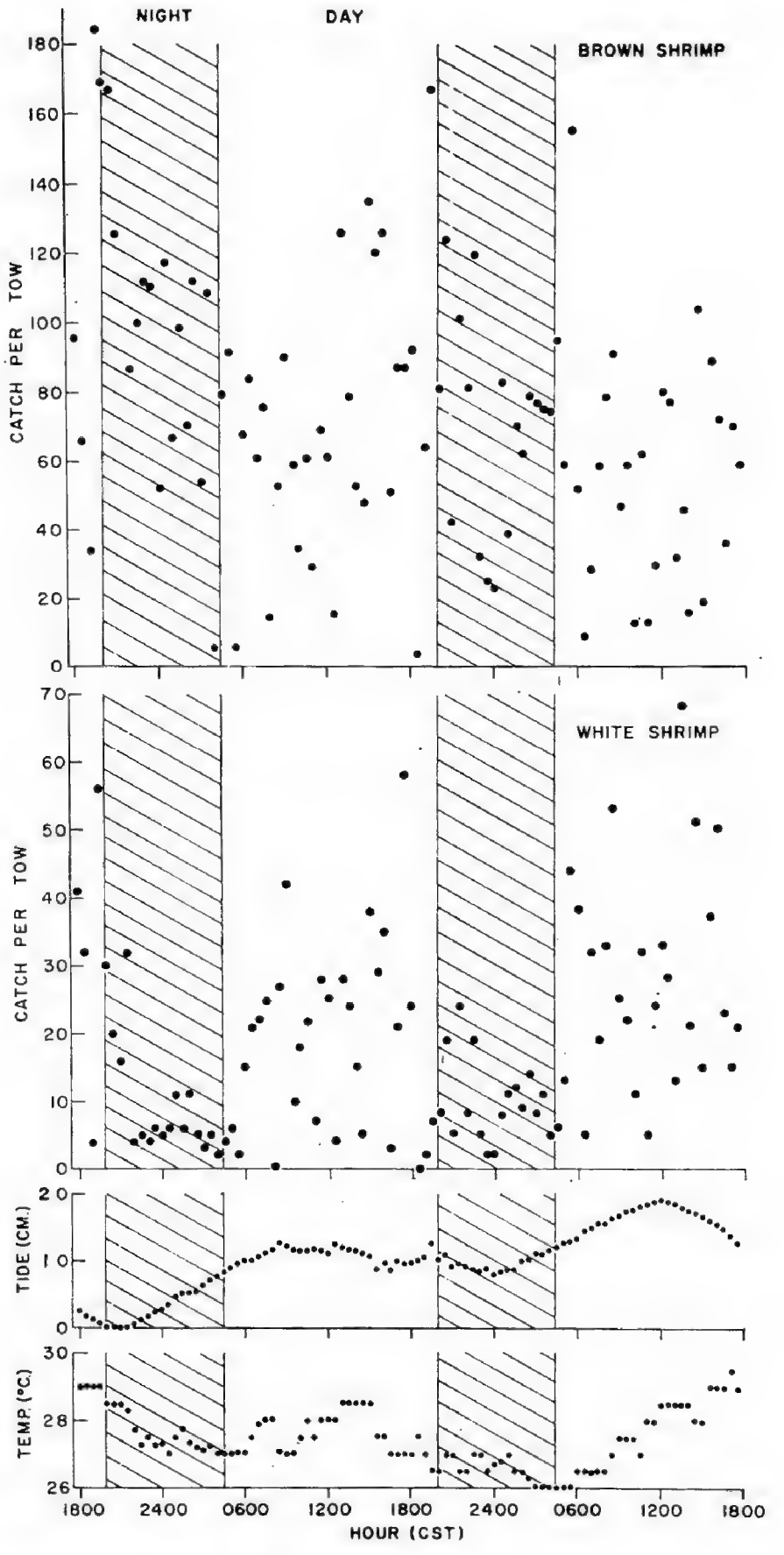

FIG. 2. Fluctuations in catches of brown and white shrimp per tow, tidal elevation (cm) and water temperature (°C) during 48 hours of sampling.

influenced catch in this species. In addition, significant ($P < 0.01$) positive correlations were found between transformed catches (Table 2) of white shrimp and tide elevation and water temperature ($r = 0.28$ and $r = 0.30$, respectively). Because tide elevation and water temperature were lower during the hours of darkness and higher during daylight hours (Fig. 2), the possible influences of these two factors are confounded with the light-dark cycle. We believe, however, that these correlations reflect a coincidence of changes in temperature and tide elevation with time of day and that white shrimp, but not brown shrimp, responded more to the light-dark cycle than to change in salinity, temperature, or tide elevation.

TABLE 1

Analysis of variance of transformed catches[a] of brown shrimp, July 6–8, 1973

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Days, D	1	0.27	0.27	2.25
Time[b], T	1	0.32	0.32	2.67
D × T interaction	1	0.10	0.10	0.83
Error	92	11.02	0.12	

[a] Log_{10} (catch). A logarithmic transformation was used to normalize the data.
[b] Light vs. darkness.

TABLE 2

Analysis of variance of transformed catches[a] of white shrimp, July 6–8, 1973

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Days, D	1	0.10	0.10	1.00
Time[b], T	1	2.24	2.24	17.23**
D × T interaction	1	0.01	0.01	0.07
Error	92	12.28	0.13	

[a] Log_{10} (catch + 1). Because some catches were zero, 1 was added to each catch prior to transformation. A logarithmic transformation was used to normalize the data.
[b] Light vs. darkness.
** Significant at $P < 0.01$.

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KEY TO THE NATANTIA (*CRUSTACEA, DECAPODA*) OF THE COASTAL WATERS ON THE TEXAS COAST

Carl E. Wood

Correction of plate appearing in *Contributions in Marine Science*. 18: p. 52, 1974.

Figures 2 and 4 on plate 6 were reversed.